

June 1976

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**A POPULATION STUDY OF VARIATION IN
DENTAL OCCLUSION**

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**Submitted in partial fulfillment
of the requirements for a
Certificate in Orthodontics**

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June 15, 1976

ACKNOWLEDGMENTS

My training in the Department of Orthodontics has been supported by a grant to Dr. Charles J. Burstone and Dr. Sam Weinstein from the National Institutes of Health, DE 00136. Additional research funds for this project were provided through DE 03729.

This work would not have been possible without years of effort by many investigators who have been interested in the populations of Bougainville Island, Papua New Guinea. All those associated with the Harvard Solomon Islands Project, and particularly, Jonathan Friedlaender, have contributed to this study.

To Patricia LeBeau, whose assistance with the computer has saved me from countless hours of aggravation, I am indebted for her help and patience.

I would like to express sincere appreciation to the members of my advisory committee, Drs. Donald Kolakowski, Andrew Poole and Sam Weinstein. They have provided generous advice and encouragement throughout the project.

The following pages are far more the work of two men than of one. Howard L. Bailit gave me access to his hard earned data, provided me with a home away from home, and variously prodded and pushed my climb from ignorance. I have learned far more from him than I would care to explain.

Finally, my wife, Linda, has once again tolerated an engrossed and preoccupied husband. Her support has provided the framework that has made this all possible.

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Part I

Problems and Methods in Research on the Genetics of Dental Occlusion

Research on the genetics of dental occlusion has had little impact on the daily practice of clinical orthodontics. Although it is recognized that genes contribute to variation in occlusion, treatment objectives and therapeutic methods do not reflect the genetic differences among individual patients. This is in spite of over 100 years of interest in the relationship between genes and occlusal variation that has continued unabated to the present time.

There are two major reasons for this lack of progress. First are the inherent limitations of genetic research on human populations. The second and more important factor has been the concept of malocclusion and some of the basic assumptions and methods used in its study by orthodontic researchers.

The purpose of this paper is to critically review the status of research on the genetics of dental occlusion, to make suggestions for the direction of future research that incorporate objectives of clinical significance and to discuss some of the methodological problems that will be encountered in such efforts.

Review of the Literature

This review will not attempt to provide a comprehensive historical perspective, or to consider all recent studies related to the genetics of occlusion. As a critical evaluation, only selected publications will be discussed. Readers interested in more bibliographic reports are referred to Weinberger,⁷⁸ Brash, McKeag and Scott,⁹ Krogman,^{41,42} Jago,⁴⁰ and Isaacson et al.³⁹

Most genetic studies of dental occlusion have been concerned with one or more of five specific objectives: (1) modes of inheritance, (2) admixture and inbreeding effects, (3) linkage analysis, (4) heritability, and (5) population differences. Prior to a discussion of each of these, it is important to note that they can be further organized into two groups; the first four, which require family pedigree data for study, and the fifth, which is based on random samples of total populations. Most orthodontic research has been concerned with family analysis and has given less consideration to the population genetics of occlusal variation. However, as will be pointed out, investigations utilizing both types of data are necessary for a thorough understanding of the genetic contribution to variation in occlusion. Each of these five issues will now be discussed in turn.

Mode of inheritance.

Most recent studies have concluded that occlusal variation is polygenic, i.e., controlled by both many genes and various environmental influences.^{32,33,47,60} This statement refers to the normal range of variation, because it is well-recognized that extreme deviation are generally due to chromosomal or single gene defects.⁶⁸ Other workers, however, have noted that strong familial similarities within normal boundaries could also be due to single

major genes.^{23,63} This may be an explanation for the famous "Hapsburg jaw" and has been suggested as the basis for Class III malocclusion in some eastern Aleut families.⁵²

The observations on human subjects have been supported by the results of animal experimentation. Studies on cattle by agricultural workers also suggest a general polygenic mode for occlusal variation⁷⁹ but demonstrate the potential for extreme effects from single pathological genes.²⁷ The possibility of single gene effects within the normal range of variation was demonstrated in a significant investigation by Gruneberg and Lea.²⁹ They found an autosomal recessive gene to cause a relatively shortened mandible and resultant retrognathia in long-haired dachshunds which otherwise remained fully viable and healthy.

Since alternative mechanisms may operate in different families, it is probably incorrect to assign a specific mode of inheritance to any type of occlusal variation. While polygenic inheritance has been emphasized in the orthodontic literature in recent years, single genes cannot be ruled out in the etiology of some of the strong similarities between sibs or parents and children that are often encountered in clinical practice.

Admixture and inbreeding effects.

Many investigators have contended that racial admixture increases the occurrence of malocclusion.^{6,26,37,43,49} In fact, the only detailed study of this possibility, conducted by Chung et al.¹³ on several thousand racially mixed children in Hawaii, concluded that human racial crossings presented no risks to dental occlusion.

Much of the opinion regarding an adverse effect of racial admixture originates in the work of Stockard and Johnston.⁷³ After examining hybrids of numerous matings between pedigreed dogs, they concluded that the length of

the upper and lower jaws were inherited independently, and that this was responsible for the "widespread disharmony in facial types commonly seen in race and breed hybrids." However, observations on highly inbred strains in which specific cranio-facial patterns have been selected for - most probably resulting in the fixation of different major genes in each breed - is of questionable relevance to the human situation.

The solitary observation concerning the effects of inbreeding on occlusal variation has been reported by Schull and Neel.⁶⁹ As part of an extensive study of inbreeding effects in Japanese children, they found some suggestion of an increased occurrence of malocclusion in the offspring of consanguinous marriages.

The studies of Chung et al.¹³ and Schull and Neel⁶⁹ together suggest that inbreeding and outcrossing have either negligible or barely detectable effects on human occlusal variation. Since these two investigations are among the largest and most sophisticated population surveys to consider variables of dental occlusion, further research in this area is unlikely to prove fruitful. The possibility cannot be excluded, however, that in other populations genes may be present that would have more significant effects when homozygous or following recombination.

Linkage analysis.

Attempts to map autosomes for major genes affecting cranio-facial variation has been limited to some preliminary observations on pathological conditions.^{41,68} This is to be expected, since the methodology involved in the detection of major genes underlying continuous variation and the linkage of these genes to mapped discrete marker traits represents the forefront of quantitative genetics in the 1970's.^{15,34,64}

As applied to dental occlusion, linkage has only been considered in

terms of the sex-chromosomes. Gorlin, Redman and Shapiro²⁵ proposed that genes on the X-chromosome cause a lengthening of the mandible relative to the maxilla, and Horowitz and Morishina³⁵ have confirmed a very high percentage of Class II relationships in XO (Turner's syndrome) subjects. However, Litton et al.⁴⁷ and Bookman et al.⁷ found no evidence of sex-linkage in their studies of Class III malocclusion, so that at this time the question remains unresolved.

Heritability.

Studies attempting to partition genetic and environmental components of variation within the cranio-facial complex have been more concerned with the facial skeleton^{31,36,38,57,58,77} and palatal dimensions^{8,67,70} than with occlusal characteristics.

In 1948, Lundstrom⁴⁸ analyzed tooth size and dental occlusion in over 200 sets of twins. In an important departure from the methodology and objectives of his predecessors, all characteristics were considered as quantitative continuous variables, so that, for example, the sagittal molar relationship was measured rather than divided into Angle's categories. Lundstrom^{50,51} has subsequently suggested that all variables examined had a larger genetic than environmental component of variation.

In a recent report, Chung and Niswander¹² have determined the correlations for several characteristics of occlusion in over 1600 pairs of sibs in Hawaii. In comparing their findings with those of Lundstrom, it is particularly interesting that in spite of very different sample populations (Hawaii and Sweden) and methods of analysis (sibs and twins), both studies found the same sequence among variables for the relative degree of genetic influence. Of the four characteristics considered by both investigations, the degree of genetic determination was greatest for the width of the upper central incisors,

and decreased in order for overjet, overbite and the sagittal molar relationship.

It should be noted that neither a twin analysis nor full sib correlations actually indicate heritability in its most useful form. Determination of the additive genetic variance, or "heritability in the narrow sense," has not been determined for any traits of dental occlusion, although Feldman and Lewontin¹⁹ consider it to be the only type of heritability estimate of use in problems of human genetics.

Population differences.

Few workers have attempted to determine the variation in dental occlusion within several populations so that objective evaluations of population differences could be made. For the most part, conclusions can only be drawn by comparing the findings of different researchers on single populations. In a recent comprehensive review of the subject, Jago⁴⁰ emphasized that the only variable common to a sufficient number of studies as to allow such comparisons on a wide basis was Angle's classification of malocclusion. However, this must be undertaken with caution, since Angle's categories are imprecisely defined and subject to considerable interpretation by independent investigators.

Nevertheless, it is clear from these studies that variation among populations does exist. The most interesting genetic difference suggested by the epidemiological data concerns the relatively high frequency of Class II and low frequency of Class III occlusion in North American Caucasian and European populations^{1,2,16,24} and the reverse situation (high frequency of Class III, low frequency of Class II) in some groups of Asian origin, including Polynesians,¹⁴ Alaskan Eskimos,⁸⁰ Aleuts,⁵³ American Indians,²⁰ and Pacific islanders in general.¹³ In addition, although environmental effects cannot be excluded, Crewe et al.²⁸ reported that the tendency toward Class II relationships

in North American Indians increased in relation to the proportion of Caucasian ancestry, and Baume³ has observed a similar effect in Polynesian-Caucasian hybrids.

These observations strongly suggest the presence of quantifiable genetic variation in the sagittal molar relationship among human populations. Specifically, they indicate the possible existence of genes skewing the distribution of molar relationships toward distoclusion in populations of recent European derivation and toward mesioclusion in selected groups with prehistoric origins in Asia.

Populations can be considered to be groups separated by time as well as by geography. Regarding the question of differences among populations in this dimension, there has been some discussion in the orthodontic literature of the effects of evolution and "civilization" on occlusal variation.⁴⁴

Long-term evolutionary changes in the dento-facial complex apparently have involved a reduction in jaw size in association with the needs of cephalization and upright posture. Because we do not have appropriate samples for a valid statistical analysis, the suggestion that there has been an increase in the occurrence of occlusal disharmonies accompanying these changes over the last 50 thousand years or so must remain essentially conjecture. If an increase in occlusal variation has taken place, it could have a genetic basis related to differential selection pressures on the size of the jaws and teeth⁷¹ or to some degree of relaxed natural selection on the facial complex.⁵⁹

A different problem is the observation that an increase in the frequency of occlusal disharmonies seems to occur within one generation after non-technological societies are introduced to Western culture.^{62,66} This change has significant clinical and manpower implications, particularly

as these underdeveloped areas increase their demand and need for dental services. However, as discussed by Niswander^{62,63} these changes seem to occur entirely too fast to be associated with genetic selection, and explanations for this observation are more likely to be found in the environment.

Problems and Some Solutions

As noted earlier, genetic questions concerning dental occlusion may be approached at two basic levels. First is the study of populations. Changes in gene frequencies through time within a single population, the maintenance of polymorphisms and the genetic differences between populations form the core of inquiry for population genetics.

The second level of study is that of individuals within families. This research is concerned with evaluating modes of inheritance, determining linkage, calculating heritability and detecting major genes. It is also at this level that genetic questions most related to clinical treatment arise.

The purpose of the following discussion is to offer some suggestions regarding the direction for future research on dental occlusion in both of these areas. The distinctions between the two are at times arbitrary, and are maintained here primarily for purposes of organization. Certain methodological problems to be discussed apply to both areas and will therefore be evaluated as they arise.

The concept of malocclusion.

Apparent from the preceeding review of the literature is the observation that genetic research on dental occlusion has primarily been concerned with the etiology and distribution of "malocclusion." In addition, most studies have considered malocclusion to be largely synonymous with Angle's classification.

There are problems with both aspects of this approach. First, the general concept of malocclusion is inconsistent with modern knowledge of the meaning and basis for variation within populations. The significance of variation among individuals and the present status of genetic theory regarding variation have been well summarized by Lewontin:⁴⁵

...the essential nature of the Darwinian revolution... necessarily takes the variation between individuals as of the essence...this emphasis on individual variation as the central reality of the living world is the mark of modern evolutionary thought and distinguishes it from the typological doctrine of previous time.

Implicit in the study of malocclusion, however, is precisely such a typological concept. "Malocclusion" clearly suggests that all variants from a specified normal are abnormal. This approach directs attention away from the analysis of variation among individuals, and in so doing, has delayed insight into the genetics of dental occlusion.

The second aspect of the problem concerns investigations which select as specific objectives for study Angle's Class II or Class III malocclusion. Difficulties arise here when a continuous variable is divided into a small number of ordinal categories which are then treated as a series of independent variables.

Class I, II and III malocclusions are clinically useful but arbitrary divisions of a continuous variable, the sagittal relationship of first permanent molars. For example, although individuals can be grouped as tall, medium or short, and standardized definitions may be adopted, this does not mean that "tallness" should be studied genetically - the appropriate variable is "height." Harris³⁰ has attempted to justify the study of each of Angle's categories as a separate variable by equating such artificially discontinuous variables with truly discontinuous characteristics. Several other aspects of dental occlusion also vary in a quantitative continuous manner and should be studied as a single unit. Incisor crowding and incisor spacing are continuous, as are posterior buccal cross-bite and posterior lingual cross-bite.

It may appear that this suggested approach to the measurement of occlusal

variation is an oversimplification of a complex problem. Class II and Class III malocclusion are not based simply upon the relationship of first molars, but upon a complex interaction of cranio-facial structures. Occlusion may in fact vary depending upon pleiotrophic effects of one or more genes on several components of the cranio-facial skeleton and/or soft tissues. However, such relationships would have little bearing on the argument that we need to study occlusal variation rather than malocclusion. Once the interactions are understood in a quantitative manner, multivariate techniques may be applicable for studying several characteristics simultaneously. Nevertheless, occlusion is still related to variation in a series of continuous characteristics and should not be interpreted on the basis of the truncated sampling which occurs when only one tail of the distribution is selected for analysis.

It is also evident that distinct "types" exist within occlusal categories. For example, subjects with Class I molar relationships but with bimaxillary prognathism will have identical measurements of the sagittal molar relationship as individuals with ideal occlusion. This indicates that many variables, in this case the relationship of the maxilla and mandible to the cranial base, need to be examined to determine the extent and nature of variation among individuals in dental occlusion.

Population variation.

If epidemiological reports of malocclusion frequencies (except for public health purposes) and genetic studies of Class II and Class III malocclusion are inappropriate objectives for study, what then are appropriate objectives?

First is the relatively simple goal of quantifying and evaluating phenotypic variance. What is needed for this purpose are random samples of diverse human populations. Defining a "population" for a quantitative genetic study can be a problem, the basic concept being that of a group of interbreeding

or potentially interbreeding individuals who share a common gene pool. In research on dental occlusion, patients from an orthodontic practice and their families, or all children in a school except those who have had orthodontic treatment are biased and inappropriate samples.

The fundamental question to be evaluated with a valid sample is how much variation actually exists in the population for the characteristics of dental occlusion. This requires a basic descriptive study of overjet, overbite, molar relationship, crossbites, crowding and spacing, malalignment and other occlusal variables, defined in an objective and replicable manner, such that means and variances can be calculated. The role of epidemiological factors such as age, sex, geography and diet can then be examined to establish their relationship to the observed variation.

After the variation within the population is described and understood, the variation between populations can be compared and the causes for observed differences evaluated. It is at this level that studies of biological distance and discrimination are of particular interest. To the extent that distance matrices based upon different sets of variables are structurally similar to each other and to linguistic, geographic and migrational matrices, insight can be gained into the relative roles of factors which affect population gene frequencies - genetic drift, gene flow and natural selection.^{10,21,22}

Methodological problems.

Having suggested that quantitative research is needed on variation in dental occlusion within and among random samples of human populations, it must be acknowledged that such an investigation will be methodologically difficult. One major problem concerns the treatment of subjects with missing teeth. Two questions are related to this problem: first, deciding whether or not to include a given individual, and second, the effects of this decision on the analysis.

After a tooth is lost, drift of adjacent teeth can occur and functional patterns may be altered. As an added environmental effect, this will tend to decrease the correlation between relatives and increase the absolute magnitude of population variation. If longitudinal data are not available to evaluate these changes, measurements can either be recorded directly from the casts, with knowledge that an added environmental component has been included, or a correction can be applied following what must be a somewhat vague judgement as to the effect of the tooth loss. However, when there are only a few remaining teeth, a subject would rarely be included in the analysis. The problem there becomes one of selecting a cut-off point, and no generally applicable solution can be offered. The ultimate decision will depend upon the frequency of tooth loss in the sample and the judgement of the investigator.

This decision, however, may have important implications. It is likely that certain occlusal variables are related to early tooth loss. For example, the loss of maxillary incisors due to trauma could be caused by a large overjet. Eliminating these subjects will therefore result in a biased sample selection, with a tendency toward exclusion of extreme values for some variables. This will not only eliminate from study some of the potentially most interesting subjects in terms of a genetic analysis (i.e., those deviating most from the mean), but will also result in lowered estimates of the magnitude of population variation.

A second major problem in population studies concerns subjects in the mixed dentition period. While changes in occlusal variables occur throughout life, once the permanent dentition is reached age adjustments may be made through the use of regression equations. However, in the mixed dentition period, arch dimensions change with the eruption of each permanent tooth.⁵⁴ Although the young school-aged subject is frequently the most accessible for

research, sample sizes will rarely be large enough to group subjects according to identical patterns of erupted teeth. Some type of compromise will usually have to be accepted. This will affect the calculation of parent-child or sib-sib correlations and the comparison of populations with different age pyramids.

A third and final methodological issue to be discussed concerns the maxillo-mandibular relationship. There are several potential positions that the mandible may assume while making contact with the maxilla,⁶⁵ and a selection from among these will affect the measurement of all interarch characteristics. However, the choices can be realistically reduced to two possible alternatives, centric occlusion (convenience occlusion, habitual occlusion) and centric relation (retruded contact position).

While centric relation is more stable, it is of questionable biological significance. Centric occlusion, although susceptible to change following the loss, movement or attrition of teeth, is probably the best single position for evaluating biting forces and occlusal function in general. In a word, based upon functional considerations, it is the phenotype. In addition, the difficulty associated with obtaining centric relation in field work and recording it on dental casts has resulted in the general use of centric occlusion by those involved in the development of indices of malocclusion^{5,74} and in recent large epidemiologic and genetic studies.^{4,13}

In most large collections of dental casts an accurate recording is not available for centric relation or for centric occlusion. A study of dental occlusion in these important collections is only possible by articulating casts in maximum intercuspation. Although this may deviate from an accurate centric occlusion recording for a small number of subjects, it is likely that on a population basis it will not result in significant problems.

Family analysis.

While the methods of population genetics and the epidemiology of occlusal variation discussed in the preceeding sections can provide information regarding the basis for differences among populations in dental occlusion, orthodontic studies have traditionally been more concerned with problems that require family data for analysis. The issues that have been raised regarding the measurement of continuous variables rather than malocclusion categories do not change for this type of investigation, and the methodological problems of missing teeth, the mixed dentition and intermaxillary relationships also apply to the following discussion.

Modes of inheritance. The prevailing conventional wisdom is that Class II and Class III malocclusions have a polygenic mode of inheritance, i.e., they are influenced by the action of many genes and environmental effects.^{32,33,47,60} This conclusion is based on several observations: (a) no simple pattern of segregating genes can be established in studies of family pedigrees, (b) cranio-facial variation is continuous, and (c) the correlation among relatives for cranio-facial variables within occlusal categories conforms to the expectations of polygenic inheritance. However, if the variation is continuous, why have subjects been grouped as only present or absent for the characteristic of interest, and, in addition, if evaluating the similarity among relatives, why not directly measure the occlusal relationship and determine its correlations? Considering the variable of interest to be the sagittal molar relationship rather than the presence or absence of Class II and Class III categories make these suggestions self-evident.

In any case, while we agree that occlusal variables are most likely polygenic, such a conclusion is unwarranted by the data that has been

presented so far.^{32,33,47} There are two reasons for the frequent misinterpretation of the available data: (a) insufficient consideration of the possible role of environmental effects, and (b) the question of the meaning of polygenic inheritance when it has in fact been demonstrated to exist.

Perhaps the most questionable simplifying assumption in the many genetic models used to evaluate modes of inheritance is the hypothesized lack of environmental co-variation among relatives. Not to be confused with Lamarkian genetics, aspects of environmental co-variation are in fact being developed into a concept of cultural inheritance by Cavalli-Sforza and Feldman.¹¹ The problem is that related individuals clearly have more similar environments than the population as a whole. For characteristics that are phenotypically plastic, i.e., affected by various environmental influences, relatives can be similar because of common environments rather than common genes. It is also well-established that a trait can be continuously distributed with only a single segregating gene if there are environmental effects.⁷⁶ Such single gene traits would correlate among relatives according to the degree of common environment, which is generally similar to the percentage of common genes, and would show no clear segregational patterns in pedigree studies. Because of the very real possibility of environmental effects, there is no justification in concluding from the available literature that occlusal variables are polygenic. We agree that a polygenic mode is most reasonable, and the weight of evidence presented to date is supportive of it. However, the data are not inconsistent with environmentally-sensitive single gene inheritance, and a valid distinction between the two models has not been presented for any cranio-facial variables.

Major genes. If occlusal variables were demonstrated to be polygenic,

what would this finding most likely mean? The assumptions of biometrical genetics require a sufficiently large number of genes to have a continuous distribution of effects. While numbers are rarely discussed, the "ball-park" estimates of many investigators would probably range from 25 to 200, since typical figures are 35 loci for the weight of mice at six weeks of age, and 99 for the number of abdominal bristles in *Drosophila*.¹⁷

With this many loci affecting a variable, what would be the next worthwhile research effort? Individual gene effects cannot be detected, so all that remains is establishing the heritability of the characteristic - how much of the variation can be attributed to genetic causes. However, while this knowledge can be of interest for several problems of evolutionary biology, it is of little consequence to any clinical decisions.¹⁹ The degree of heritability has little if any bearing on how successful clinical procedures will be. Contrary to common opinion, the extent to which genes determine a trait has no relationship whatsoever with the success of environmental intervention.^{18,46,55} In addition, it will have no bearing on the type of treatment, nor will it be of much use in genetic counseling. For the specific orthodontic problem of predicting growth changes, the value of variables can be determined without any reference to their heritability.

Beyond these issues, Lewontin⁴⁶ and Feldman and Lewontin¹⁹ have raised important questions about the validity of linear models for the partitioning of variance components. While debate on this problem continues,⁵⁶ it is important to point out that the manner in which genotype-environment interactions change in their effect on the phenotype over the range of environments and genotypes (their "norm of reaction") may mean that the whole effort has been "the endless search for better methods of estimating useless quantities."⁴⁶

If, therefore, occlusal variation was demonstrated to be polygenic, and this meant large numbers of segregating genes, there would be little of value that genetics could contribute to clinical orthodontics, except in the area of severe chromosomal anomalies.

Fortunately, this is probably not the case. Whenever the number of genes affecting polygenic traits has actually been determined, a remarkably small number have been found.⁷⁶ The biometric estimate of 99 loci for abdominal bristle number in *Drosophila* is in actuality five loci accounting for 85% of the difference between high and low lines.⁷⁵ Human skin color seems to be controlled by only 3 or 4 loci.^{61,72} As discussed by Thompson⁷⁶ this lower number of genes is much more compatible with estimates of the total number in the genome. Furthermore, these genes are not all of equal significance. This raises the possibility, which Thoday⁷⁵ emphasized as the next major goal for human genetics, of locating and studying genes within the normal range of continuous variation.

Until recently, major genes (single genes whose effects could be observed phenotypically) were considered to be of two types - pathological and polymorphic.⁷⁵ The pathological referred to extreme deviants (eg., achondroplasia) and the polymorphic to distinct normal categories (eg., the ABO blood cell antigens). Recently a new type of major gene has been recognized - but it can only be "seen" by the computer in a statistical analysis. These are genes with large effects within the normal range of variation, and efforts by a number of investigators now make it possible to detect the presence of such genes by segregation and linkage analysis.^{15,34,64}

As Lewontin⁴⁶ has suggested, it is possible that clinical treatment will vary depending upon alternative causes for a disorder. (This is a different problem than the relative contributions of an interacting genotype and

environment, i.e., heritability.) Pathological major genes may act as a locus independent of the segregating genes normally affecting the variation of a character. In this sense, a single gene "overrides the system" and produces an effect regardless (or greatly modifying) what has been inherited by the polygenic system. The study of extreme variants, particularly if related to single genes, is the one circumstance noted earlier in which a typological study of Class II or Class III occlusion would be appropriate. However, the response need not be so dramatic as to produce only extreme manifestations.⁶³ It is possible that many strong familial similarities are due to single major genes running in a family but not widely distributed in the population. Therefore, the possibility of establishing different causes exists within the range of normal variation as well as for the occurrence of extreme phenotypes.

In summary, it is suggested that there is the possibility of detecting two types of major genes underlying continuous variation. First are alleles with large effects at loci which normally segregate for a characteristic, and second would be a gene at a single pathological (or "familial") locus but producing an effect within the normal range of variation. Although application will not be in the immediate future, detection of these genes holds the promise of substantial contributions to clinical practice. Once major genes are located, their biochemical products can be studied. This data may ultimately be of use in accurate predictions of long-term growth changes and direct biochemical methods for clinical intervention.

It may seem that such objectives are highly speculative; particularly if it should be found that anatomical variation is based more upon regulatory gene control at the transcriptional level than upon differences in structural proteins, success in controlling and predicting occlusal variation will be in the more distant future. At the very least, however, a rationale has been

developed with a long-range goal of contributing to the direct solution of clinical problems. No more, and perhaps less, has been achieved over the past 50 years.

Summary and Conclusions

Research on the genetics of dental occlusion has traditionally been based upon the concept of "malocclusion." Although of recognized clinical value, the biological validity of the various categories of malocclusion is questionable. Genetic research should instead center upon concepts related to continuous variables and population variation.

The magnitude of variation for the characteristics of dental occlusion needs to be quantified within diverse human populations. The relationship of this variation to epidemiological factors and the nature of differences among populations are also areas in need of much investigation.

This type of research will face methodological problems not encountered in studies of malocclusion. Measurements taken on subjects with missing teeth provide a potential source of bias that must be carefully evaluated, since these subjects cannot simply be excluded from study without resulting in an alternative type of bias. The potential intermaxillary relationships appropriate for study are centric relation and centric occlusion. While centric relation has an advantage in stability, it is suggested that centric occlusion (convenience occlusion) is the functional phenotype and therefore the most appropriate position from which to take measurements.

Several recent studies stress a polygenic mode of inheritance for the characteristics of dental occlusion. The evidence is reviewed and evaluated, and it is concluded that although a polygenic mode is most likely, there is insufficient data to exclude the possibility of environmentally-sensitive single gene inheritance.

If occlusion is demonstrated to be polygenic, studies attempting to partition environmental and genetic causes of variance will contribute little to clinical problems. Long-term objectives should instead center upon the

detection of major genes and determination of their biochemical action.

References

1. Adler, P.: The incidence of dental caries in adolescents with different occlusions. J. Dent. Res., 35:344-349, 1956.
2. Ast, D.B., Carlos, J.P. and Cons, N.C.: The prevalence and characteristics of malocclusion among senior high school students in upstate New York. Am. J. Orthodont., 51:437-445, 1965.
3. Baume, L.J.: Uniform methods for the epidemiologic assessment of malocclusion. Results obtained with the World Health Organization standard methods (1962 and 1971) in South Pacific populations. Am. J. Orthodont., 66:251-272, 1974.
4. Baume, L.J. and Marechaux, S.C.: Uniform methods for the epidemiologic assessment of malocclusion. Am. J. Orthodont., 66:121-129, 1974.
5. Baume, L.J., Horowitz, H.S., Summers, C.J., Backer Dirks, O., Brown, W.A.B., Carlos, J.P., Cohen, L.K., Freer, R.J., Harvold, E.P., Moorrees, C.F.A., Salzmann, J.A., Schmuth, G., Solow, B. and Taatz, H.: A method for measuring occlusal traits. Int. Dent. J., 23:530-537, 1973.
6. Bjork, A.: Some biological aspects of prognathism and occlusion of the teeth. Acta Odont. Scand., 9:1-40, 1950.
7. Bookman, D.J., DeMuth, D.L., Dulaney, H.L., George, D.C., Haller, E.L., Marconi, F.I., Massignan, D.E., Trojan, T.M. and Vedder, J.L.: Inheritance of the craniofacial complex in Class III malocclusion. Unpublished Master's thesis (orthodontics), Ann Arbor, University of Michigan. 1974.
8. Bowden, D.E.J. and Goose, D.H.: The inheritance of palatal arch width in human families. Arch. Oral Biol., 13:1293-1295, 1968.
9. Brash, J.C., McKeag, H.T.A. and Scott, J.H.: The Aetiology of Irregularity and Malocclusion of the Teeth, 2nd Ed. London, Dental Board of the United Kingdom, 1956.

10. Brewer-Carias, C.A., LeBlanc, S. and Neel, J.V.: Genetic structure of a tribal population, the Yanomama Indians. XIII. Dental microdifferentiation. Am. J. Phys. Anthropol., 44:5-14, 1976.
11. Cavalli-Sforza, L.L. and Feldman, M.W.: Cultural versus biological inheritance: phenotypic transmission from parents to children (a theory of the effect of parental phenotypes on children's phenotypes). Am. J. Hum. Genet., 25:618-637, 1973.
12. Chung, C.S. and Niswander, J.D.: Genetic and epidemiologic studies of oral characteristics in Hawaii's schoolchildren. V. Sibling correlations in occlusion traits. J. Dent. Res., 54:324-329, 1975.
13. Chung, C.S., Niswander, J.D., Runck, D.W., Bilben, S.E. and Kau, M.C.W.: Genetic and epidemiologic studies of oral characteristics in Hawaii's schoolchildren. II. Malocclusion. Am. J. Hum. Genet., 23:471-495, 1971.
14. Davies, G.N.: Dental conditions among the Polynesians of Pukapuka (Danger Island). I. General background and the prevalence of malocclusion. J. Dent. Res., 35:115-131, 1956.
15. Elston, R.C. and Stewart, J.: A general model for the genetic analysis of pedigree data. Human Hered., 21:523-542, 1971.
16. Emrich, R.E., Brodie, A.G. and Blayney, J.R.: Prevalence of Class I, Class II and Class III malocclusions (Angle) in an urban population. An epidemiological study. J. Dent. Res., 44:947-953, 1965.
17. Falconer, D.S.: Introduction to Quantitative Genetics. New York, Ronald Press, 1960.
18. Falconer, D.S.: The inheritance of liability to certain diseases, estimated from the incidence among relatives. Ann. Hum. Genet., 29:51-76, 1965.
19. Feldman, M.W. and Lewontin, R.C.: The heritability hang-up. Science, 190:1163-1168, 1975.

20. Foster, L.W.: Dental conditions in White and Indian children of Northern Wisconsin. J. Am. Dent. Assoc., 29:2251-2255, 1942.
21. Friedlaender, J.S., Sgaramella-Zonta, L.A., Kidd, K.K., Lai, L.Y.C., Clark, P. and Walsh, R.J.: Biological divergences in South-Central Bougainville: An analysis of blood polymorphism gene frequencies and anthropometric measurements utilizing tree models, and a comparison of these variables with linguistic, geographic and migrational "distances." Am. J. Hum. Genet., 23:253-270, 1971.
22. Friedlaender, J.S.: Patterns of Human Variation. The Demography, Genetics and Phenetics of Bougainville Islanders. Cambridge, Harvard Univ. Press, 1975.
23. Goodman, H.O.: Genetic parameters of dentofacial development. J. Dent. Res., 44:174-184, 1965.
24. Goose, D.H., Thomson, D.G. and Winter, F.C.: Malocclusion in school children of the West Midlands (England). Brit. Dent. J., 102:174-178, 1957.
25. Gorlin, R.J., Redman, R.S. and Shapiro, B.L.: Effect of X-chromosome aneuploidy on jaw growth. J. Dent. Res., 44:269-282, 1965.
26. Graber, T.M.: Orthodontics. Principles and Practice, 2nd Ed. Philadelphia, W.B. Saunders Co., 1966.
27. Gregory, K.E., Koch, R.M. and Swiger, L.A.: Malocclusion - a hereditary defect in cattle. J. Hered., 53:168-170, 1962.
28. Grewe, J.M., Cervenka, J., Shapiro, B.L. and Witkop, C.J. Jr., Prevalence of malocclusion in Chippewa Indian children. J. Dent. Res., 47:302-305, 1968.
29. Gruneberg, H. and Lea, A.J.: An inherited jaw anomaly in long-haired dachshunds. J. Genet., 39:285-296, 1940.
30. Harris, J.E.: Problems in the statistical inspection of cranio-facial variables during growth and development. In Moyers, R.E. and Krogman, W.M. (eds): Cranio-facial Growth in Man. Oxford, Pergamon Press, 1971.

31. Harris, J.E., Kowalski, C.J. and Watnick, S.S.: Genetic factors in the shape of the craniofacial complex. Angle Orthodont., 43:107-111, 1973.
32. Harris, J.E., Kowalski, C.J. and Walker, S.J.: Intrafamilial dentofacial associations for Class II Division 1 probands. Am. J. Orthodont., 67:563-570, 1975.
33. Harris, J.E., Kowalski, C.J. and Walker, S.J.: Dentofacial differences between "normal" sibs of Class II and Class III patients. Angle Orthodont., 45:103-107, 1975.
34. Haseman, J.K. and Elston, R.C.: The investigation of linkage between a quantitative trait and a marker locus. Behav. Genet., 2:3-19, 1972.
35. Horowitz, S.L. and Morishima, A.: Palatal abnormalities in the syndrome of gonadal dysgenesis and its variants and in Noonan's syndrome. Oral Surg., 38:839-844, 1974.
36. Horowitz, S.L., Osborne, R.H. and DeGeorge, F.V.: A cephalometric study of craniofacial variation in adult twins. Angle Orthodont., 30:1-5, 1960.
37. Hunt, E.E. Jr.: Malocclusion and civilization. Am. J. Orthodont., 47:406-422, 1961.
38. Hunter, W.S.: A study of the inheritance of craniofacial characteristics as seen in lateral cephalograms of 72 like-sexed twins. Trans. Europ. Orthodont. Soc., 41:55-70, 1965.
39. Isaacson, R.J., Christiansen, R.L., Evans, C.A. and Riedel, R.A.: Research on variation in dental occlusion. Am. J. Orthodont., 68:241-255, 1975.
40. Jago, J.D.: The epidemiology of dental occlusion; a critical appraisal. J. Pub. Health Dent., 34:80-93, 1974.
41. Krogman, W.M.: The role of genetic factors in the human face, jaws and teeth: a review. Eugen. Rev., 59:165-192, 1967.

42. Krogman, W.M.: Craniofacial growth and development: an appraisal.
Yrbk. Phys. Anthropol., 18:31-64, 1974.
43. Lavelle, C.L.B.: Maxillary and mandibular tooth size in different racial groups and in different occlusal categories. Am. J. Orthodont., 61:29-37, 1972.
44. Lavelle, C.L.B.: A study of multiracial malocclusions. Community Dent. Oral Epidemiol., 4:38-41, 1976.
45. Lewontin, R.C.: The Genetic Basis of Evolutionary Change. New York, Columbia Univ. Press, 1974.
46. Lewontin, R.C.: The analysis of variance and the analysis of causes. Am. J. Hum. Genet., 26:400-411, 1974.
47. Litton, S.F., Ackerman, L.V., Isaacson, R.J. and Shapiro, B.L.:
A genetic study of Class III malocclusion. Am. J. Orthodont., 58:565-577, 1970.
48. Lundstrom, A.: Tooth Size and Occlusion in Twins. New York, S. Karger, 1948.
49. Lundstrom, A.: The aetiology of crowding of teeth (based on studies of twins and from morphological investigations) and its bearing on orthodontic treatment. Trans. Europ. Orthodont. Soc., 176-191, 1951.
50. Lundstrom, A.: The significance of genetic and nongenetic factors in the profile of the facial skeleton. Am. J. Orthodont., 41:910-916, 1955.
51. Lundstrom, A.: Aetiology and prevention of malocclusion. In Lundstrom, A. (ed), Introduction to Orthodontics. New York, McGraw-Hill Book Co., 1960.
52. Moorrees, C.F.A.: The dentition as a criterion of race with special reference to the Aleut. J. Dent. Res., 30:815-821, 1951.
53. Moorrees, C.F.A.: The Aleut Dentition. Cambridge, Harvard Univ. Press, 1957.

54. Moorrees, C.F.A.: The Dentition of the Growing Child. Cambridge, Harvard Univ. Press, 1959.
55. Morton, N.E.: Analysis of family resemblance. I. Introduction. Am. J. Hum. Genet., 26:318-330, 1974.
56. Morton, N.E.: Analysis of family resemblance and group differences. Soc. Biol., 22:111-116, 1975.
57. Nakata, M., Yu, P.L. and Nance, W.E.: Multivariate analysis of craniofacial measurements in twin and family data. Am. J. Phys. Anthropol., 41:423-430, 1974.
58. Nakata, M., Yu, P.L., Davis, B. and Nance, W.E.: Genetic determinants of cranio-facial morphology: a twin study. Ann. Hum. Genet., 37:431-443, 1974.
59. Neel, J.V. and Salzano, F.M.: Further studies on the Xavante Indians. X. Some hypotheses-generalizations resulting from these studies. Am. J. Hum. Genet., 19:554-574, 1967.
60. Nelson, M.M.: A brief study of the genetics of malocclusion. Trans. Europ. Orthodont. Soc., 55-68, 1969.
61. Nicholls, E.M.: Pigment spotting in man and the number of genes determining skin and eye color. Human Hered., 23:1-12, 1973.
62. Niswander, J.D.: Further studies on the Xavante Indians. VII. The oral status of the Xavantes of Simeos Lopes. Am. J. Hum. Genet., 19:543-553, 1967.
63. Niswander, J.D.: Genetics of common dental disorders. Dent. Clin. N.A., 19:197-206, 1975.
64. Ott, J.: Estimation of the recombination fraction in human pedigrees: efficient computation of the likelihood for human linkage studies. Am. J. Hum. Genet., 26:588-597, 1974.

65. Posselt, U.: The Physiology of Occlusion and Rehabilitation, 2nd Ed. Philadelphia, F.A. Davis Co., 1968.
66. Price, W.A.: Studies of relationships between nutritional deficiencies and (a) facial and dental arch deformities and (b) loss of immunity to dental caries among South Sea Islanders and Florida Indians. Dent. Cosmos, 77:1033-1045, 1935.
67. Riquilme, A. and Green, L.J.: Palatal width, height and length in human twins. Angle Orthodont., 40:71-79, 1970.
68. Salzmann, J.A.: Effect of molecular genetics and genetic engineering on the practice of orthodontics. Am. J. Orthodont., 61:437-472, 1972.
69. Schull, W.J. and Neel, J.V.: The Effects of Inbreeding on Japanese Children. New York, Harper and Row, 1965.
70. Shapiro, B.L.: A twin study of palatal dimensions partitioning genetic and environmental contributions to variability. Angle Orthodont., 39:139-151, 1969.
71. Sofaer, J.A., Bailit, H.L. and MacLean, C.J.: A developmental basis for differential tooth reduction during hominid evolution. Evolution, 25:509-517, 1971.
72. Stern, C.: Model estimates of the number of gene pairs involved in pigmentation variability of the Negro-American. Human Hered., 20:165-168, 1970.
73. Stockard, C.R. and Johnson, A.L.: The Genetic and Endocrinic Basis for Differences in Form and Behavior. Philadelphia, Wistar Institute, 1941.
74. Summers, C.J.: The occlusal index: a system for identifying and scoring occlusal disorders. Am. J. Orthodont. 59:552-567, 1971.
75. Thoday, J.M.: New insights into continuous variation. In Proc. 3rd Int. Cong. Hum. Genet. Baltimore, Johns Hopkins Press, 1967.

76. Thompson, J.N. Jr.: Quantitative variation and gene number. Nature, 258:665-668, 1975.
77. Watnick, S.S.: Inheritance of craniofacial morphology. Angle Orthodont., 42:339-351, 1972.
78. Weinberger, B.W.: Orthodontics. An Historical Review of its Origin and Evolution. St. Louis, C.V. Mosby, 1926.
79. Wiener, G. and Gardner, W.J.F.: Dental occlusion in young bulls of different breeds. Anim. Prod., 12:7-12, 1970.
80. Wood, B.F.: Malocclusion in the modern Alaskan Eskimo. Am. J. Orthodont., 60:344-354, 1971.

Part II

Variation in Dental Occlusion and Arches among Melanesians of Bougainville Island, Papua New Guinea.

I. Methods, Age Changes, Sex Differences and Population Comparisons.

Dental occlusion and the size and shape of the dental arches have been of importance in taxonomic assignments within the paleoanthropological record (Simons and Pilbeam, 54; Walker and Andrews, 73). The interpretive value of these characteristics would be increased by knowledge of the magnitude of variation within and among extant populations and an understanding of the genetic basis and functional significance for this variation.

It is somewhat surprising, therefore, that variation in dental occlusion has received little attention in the anthropological literature. Instead, interest has generally focused on population frequencies of "malocclusion" categories. However, this concept of clinical orthodontics involves a typological decision, in which all variants from a specified normal are considered to be abnormal. Such an approach to variation within a species is widely recognized to be inconsistent with modern precepts of evolutionary biology. The characteristics of dental occlusion should instead be defined on an interval scale, which would allow the use of parametric statistics in the study of occlusal variation as a normal population characteristic.

The purpose of this paper is to report on a population study of variation in occlusion. In addition to basic descriptive data, the contribution of age and sex to variation will be examined, and available published findings will be summarized to evaluate some of the factors contributing to differences among populations. The group selected for study are the non-Austronesian speaking Melanesians of Bougainville Island, Papua New Guinea, on whom an extensive data base of biological variation has already been developed (Friedlaender, 69, 75; Friedlaender et al., 71; Bailit et al., 68a).

MATERIALS AND METHODS

Sample selection.

Bougainville is the northernmost island of the Solomon chain in the south Pacific, within the area recognized as Melanesia. It has a maximum length of 126 miles and an average width of 30 miles, with a total population of approximately 70,000. The ecology of the island has been described in detail by Oliver (55).

Since a taro blight in the early 1950's, sweet potatoes have been the primary food staple. The chewing of betel nuts and pipe smoking occur with varying frequency throughout the island. Dental treatment is limited to extractions by a medical orderly in the larger villages. More comprehensive care is available to some individuals from a dentist who makes an annual or semi-annual visit to the district capital, Kieta. Additional information on dietary practices may be found in Friedlaender (69, 75) and the oral health status has been described by Bailit et al. (68a, 68b).

In 1966, Friedlaender (69, 75), as part of the Harvard Solomon Islands Expedition (Damon, 73), made a serological and anthropometric survey along a 60 mile range in the central region of the island. Dental casts in the same villages were collected by Bailit in 1970 and merged with the genealogical data from the earlier expedition. Ascertainment was close to complete in all villages except for children with no permanent teeth, older individuals who were edentulous or had loose teeth that might be extracted by the impression procedure, and some young adult males who were absent from the villages for employment. All casts were poured in dental stone immediately after impressions were taken. For some older subjects, the age determinations, which were based on Catholic Mission records, physical examinations and genealogical relationships, can only be considered accurate to within five years.

In the present report, twelve villages¹ comprising four non-Austronesian (Papuan) "languages" have been combined as a single sample for analysis. Although this area demonstrates a high degree of isolation by distance (Friedlaender, 71), some gene flow between all villages takes place (Friedlaender, 69, 75), and environmental conditions are generally similar. From the standpoint of the global range of human variation, the current group can be considered a single population. Future analysis will examine microevolutionary variation between the villages.

Data collection and measurement reliability.

Measurements were taken by a single investigator (RJS). Helios dial calipers calibrated to 0.05 mm were used for all measurements except overjet, which can be measured more accurately with a groove micrometer (Mitutoyo Corp., Mini-Mike series 146). All measurements were taken to the nearest 0.1 mm, resulting in 30 to 300 intervals over the range of values for each quantitative variable, as suggested by Sokal and Rohlf (69).

Repeated measurements on a series of 20 casts resulted in a standard error of measurement ranging from 0.014 mm for midline diastema to a maximum of 0.17 mm for maxillary canine arch width, comparing favorably with the error estimates of previous investigators (Lundstrom, 48). Analysis of variance of repeated measures within individuals compared with measurements between individuals were all significant at $P < .001$, suggesting that measurement error would not interfere with the detection of individual differences.

Measurement was generally limited to individuals with complete dentitions, defined as the presence of all permanent teeth, with or without third molars. Some of the consequences of this non-random sampling have been discussed previously (Smith and Bailit, 76); the primary justification being that tooth

loss acts as an added environmental component of variation, allowing drift of adjacent teeth and changes in occlusal patterns.

After completion of data collection, recording and measuring errors were checked with the Churchill Editing Program (63). Using the conservative criteria of 2.50 standard errors from values predicted by multiple regression equations, over 26% of all casts had at least one variable that required remeasurement. Less than 0.1% of all measurements were found to be in error.

Variable definitions.

The variables selected can be grouped into two general categories, the first concerned with the characteristics of dental occlusion and the second with the size and shape of the dental arches. Occlusion consists of the relationship between the teeth of the opposing dental arches and with crowding, spacing and malalignment within each arch, while the size and shape of the dental arches refers to more traditional anthropometric qualities. Although soft tissue and craniofacial skeletal variation are also important in understanding occlusal variation, the available data restricted analysis to characteristics that could be reliably determined from dental casts.

The variables examined and their definitions are as follows:

Molar relationship: Angle's (1899) classification of occlusion based upon the relationship between upper and lower first permanent molars has been the most universally applied measurement in studies of dental occlusion, and its continued use is justified on the basis of the comparative data already available. Briefly, Angle's Class I indicates a relationship between maxillary and mandibular first molars in which the mesio-buccal cusp of the maxillary molar occludes with the buccal groove of the mandibular molar. In a Class II relationship, the mandibular molar is one-half cusp or more distal to the Class I position while in Class III, it is one-half cusp or more

mesial to the Class I position. The Class II category is further divided into Division 1, with labially flared maxillary central incisors, and Division 2, with lingually tipped maxillary central incisors.

However, it is also desirable to measure the sagittal molar relationship in a manner reflecting its continuous variation. This has been defined as the distance in the sagittal plane between the mesial contact points of the upper and lower first permanent molars (Seipel, 46). When the lower molar was mesial to the upper molar, the distance was positive, when distal to the upper molar, negative. The measurement was taken on both sides and averaged for each individual.

Anterior overbite - openbite: This relationship was defined as the vertical distance from the incisal edge of the maxillary central incisor to the incisal edge of the corresponding mandibular central incisor (Baume et al., 73). When the incisors overlapped (overbite), the distance was positive. When a space existed between the incisal edges in the frontal plane (openbite), the distance was negative. The measurement was taken separately for each pair (left and right) of central incisors and averaged for each individual.

Overjet: Overjet was the horizontal distance from the most labial point on the maxillary central incisor to the corresponding mandibular incisor, parallel to the occlusal plane (Baume et al., 73). If the incisors were in cross-bite, the measurement was negative. The average of left and right sides was taken for each individual.

Maxillary midline diastema: A space between the mesial surfaces of the maxillary central incisors in the frontal plane was measured when present. The distance was measured at the level of the gingival margin (Baume et al., 73).

Anterior spacing-crowding: Attempts to accurately measure this characteristic were found to have low reliability during an initial trial series of measurements. An arbitrarily defined ordinal scale with seven categories was selected and scored as follows: severe crowding = -3, moderate crowding = -2, slight crowding = -1, ideal = 0, slight spacing = +1, moderate spacing = +2 and severe spacing = +3. For statistical purposes, we assume that there is an equal distance between intervals. The anterior segment was defined as the portion of the dental arch between the mesial contact points of the left and right canines (Moorrees, 59).

Rotations and displacements from arch form: Recent efforts to characterize occlusal variations for public health purposes (Summers, 71) suggested measuring these characteristics by assigning teeth to arbitrarily defined major and minor categories and arriving at a total score by giving each minor deviation a value of one and major deviation a value of two. Minor deviations were defined as rotations greater than 15° and less than 45° or deviations between 1 and 2 mm from arch form. Major deviations were greater than 45° of rotation or greater than 2 mm displacement from arch form. Separate deviation scores were recorded for the maxillary and mandibular arches.

Posterior cross-bite: The number of maxillary premolars and first and second molars in buccal or lingual cross-bite were counted. Buccal cross-bite was defined as the lingual cusp of a maxillary tooth lying buccal to the maximum height of a buccal cusp of an opposing tooth. Lingual cross-bite as defined as a buccal cusp of a maxillary tooth lying lingual to the maximum height of a buccal cusp of an opposing tooth (Baume et al., 73). Each tooth in lingual cross-bite was scored as -1, in buccal cross-bite as +1. These can be summed to derive a total score. However, since most individuals were found to exhibit no cross-bites, mean values would be misleading. Separate

frequencies for lingual and buccal cross-bite are therefore reported in the results.

Posterior openbite: This was defined as a vertical space between the premolars or molars of the maxillary and mandibular arches. Openbite was recorded only if there was no overlap of cusps, i.e., if visible vertical space existed between the teeth (Baume et al., 73). It was measured as the maximum vertical space apparent in the sagittal plane.

Canine openbite: A preliminary survey of the casts indicated that a number of subjects displayed attrition and openbite between the maxillary and mandibular lateral incisors and canines, not involving the central incisors or posterior teeth. This has been attributed to pipe-smoking habits (Lombardi and Bailit, 72). It was measured using the same criteria of visible vertical space as defined above for posterior openbite. If an openbite included both posterior and canine teeth, it was recorded in the posterior openbite category only.

Arch width: Arch width was measured at both the first molars and canines in the maxillary and mandibular arches. It was defined as the maximum distance between buccal surfaces (Keith, 24; Meredith and Cox, 54; Knott, 61). In order to measure at a consistent point on each individual and to minimize the effects of occlusal attrition or gingival recession, the width was measured at the height of contour of the buccal surfaces, even when the width was greater at the occlusal or gingival margins.

Arch length: Arch length was defined as the linear distance from the mesial edge of the central incisor to the disto-buccal edge of the first molar (Moorrees and Reed, 54). The left and right measurements were averaged for each arch.

Calculated variables: In order to provide some indication of variation

in arch shape, the following ratios were calculated for each individual from the variables defined above:

1. Maxillary and mandibular arch shape.

$$\frac{\text{Arch length}}{\text{Molar arch width}} \times 100$$

2. Maxillary and mandibular arch width ratio.

$$\frac{\text{Canine arch width}}{\text{Molar arch width}} \times 100$$

Data analysis.

Descriptive statistics and univariate analyses were calculated using programs of the SPSS package (Nie et al., 70). Trend analysis of each variable with age was examined up to third-degree polynomials by adding age, age² and age³ in a step-wise manner to the multiple regression routine. The significance of each step was evaluated primarily by an F ratio for testing the increment in variance explained by each degree of the polynomial (Kerlinger and Pedhazer, 73).

RESULTS

Population sample.

Dental casts were obtained from 812 adults living in twelve villages. From this group, 134 (16.5%) were not measured because of missing teeth, leaving a total of 678 subjects included in the analysis. The percentage of individuals with missing teeth increased with age (Table 1).

Of the 678 subjects with complete dentitions, age estimates were not available for 157. These individuals were included in the calculation of all data except for the analysis of the age-changes themselves. The mean ages of males and females, 29.6 and 28.4 years respectively, do not differ significantly ($P > .05$). The population pyramid displays an atypical constriction between 20 and 30 years of age, corresponding to a decreased birth and infant survival rate during World War II.

Variation and sex differences.

The means, standard deviations and ranges for occlusal variables are summarized in Table 2 and for arch measurements in Table 3. The only occlusal variable to significantly differ between the sexes is the sagittal molar relationship. This may be partially accounted for by a sex difference of approximately 0.5 mm in the mesio-distal diameter of the first permanent molars (Baillit et al., 68a). In both sexes, the lower arch tends to have more rotated and displaced teeth and greater crowding of the incisors than the upper arch, confirming the observations of Helm (68) and Lombardi and Baillit (72).

As expected, the length and width of the dental arches (Table 3) are significantly larger in males ($P < .01$). The differences in mean arch shape are also significant, and suggest that the length of both the maxillary and

Table 1

**The Age and Sex Distribution of
All Subjects with Permanent Dentitions**

Age	Subjects with Complete Dentitions ¹		Subjects with Missing Teeth ²		% Excluded because of Missing Teeth ³
	M	F	M	F	
10-14	30	39	4	0	5.48
15-19	54	49	2	3	4.63
20-24	18	33	2	1	5.55
25-29	12	28	1	1	4.76
30-34	38	37	3	3	7.41
35-39	28	39	8	6	17.28
40-44	29	31	15	5	25.00
45-49	15	7	7	5	35.29
50-54	10	8	17	5	55.00
55-59	5	4	3	2	35.71
60-64	2	3	4	5	64.28
65-69	1	1	0	1	33.33
Total	242	279	66	37	

¹ Age estimates are not available on 77 of 319 males and 80 of 359 females with complete dentitions.

² Age estimates are not available on 15 of 81 males and 16 of 53 females with missing teeth.

³ Subjects with missing teeth (males and females combined) as a percentage of all individuals at each age ($\# \text{ Missing} / (\# \text{ Missing} + \# \text{ Present}) \times 100$).

Table 2
Occlusion, by Sex

Variables ¹	Males (N=319)			Females (N=359)		
	\bar{X}	S.D.	Range	\bar{X}	S.D.	Range
Molar relationship ²	2.46	1.27	-4.9 - 5.9	2.16	1.08	-1.3 - 5.7
Overjet ²	2.57	1.36	-1.8 - 12.4	2.49	1.12	-2.4 - 6.6
Anterior overbite-openbite ²	2.43	1.64	-3.5 - 7.2	2.59	1.45	-0.9 - 6.5
Upper anterior crowding-spacing	-0.33	1.20	-3.0 - 3.0	-0.20	1.30	-3.0 - 3.0
Lower anterior crowding-spacing	-0.74	1.02	-3.0 - 2.0	-0.67	1.17	-3.0 - 3.0
Upper rotations and displacements	1.37	1.60	0 - 9.0	1.41	1.68	0 - 10.0
Lower rotations and displacements	2.23	1.97	0 - 9.0	2.10	2.07	0 - 10.0

¹ All variables in mm. except anterior crowding-spacing and rotation and displacement scores.
See measurement definitions for these scales.

² Mean of measurement of right and left sides for each subject.

Table 3

Arch Measurements, by Sex

Variables ¹	Males (N=319)		Females (N=359)	
	\bar{X}	S.D.	\bar{X}	S.D.
Upper canine arch width	41.78	2.27	40.79	2.16
Upper molar arch width	61.33	2.66	58.93	2.63
Lower canine arch width	32.64	1.86	31.35	2.11
Lower molar arch width	56.71	2.56	54.65	2.50
Upper arch length ²	47.27	2.16	45.79	1.99
Lower arch length ²	43.10	1.89	41.99	1.93
Upper arch shape	77.17	3.89	77.77	3.35
Lower arch shape	76.12	3.90	76.91	3.57
Upper width ratio	68.16	3.34	69.25	2.99
Lower width ratio	57.62	3.27	57.39	3.40

¹ All variables in mm. except arch shape and width ratios.

² Mean of measurement of right and left sides for each subject.

mandibular arches are greater in females than in males for a given width at the first molars.

The number of individuals with other selected occlusal anomalies are summarized in Table 4. Both buccal and lingual posterior cross-bites are more common in men, canine and posterior openbites occur more often in women. The frequency of Angle's categories of malocclusion are presented in Table 5.

Several variables deviate from normality in their distribution. All significant deviations in clustering are leptokurtic in nature, indicating a decreased magnitude of dispersion about the mean. This is observed in both sexes for molar relationship, overjet, upper rotations and displacements, mandibular arch length, and the upper and lower arch shape ratios. The most highly skewed variables are the molar relationship, overjet, and the rotation and displacement scores of both arches. A negative (tail to the left) skewness for the sagittal molar relationship and positive skewness for overjet are consistent with the more frequent and extreme expression of distocclusion as opposed to mesiocclusion in this population. Rotation and displacement scores are skewed to the right, indicating the presence of a number of subjects with highly irregular alignment.

Differences between the sexes also exist in the magnitude of variation for some variables, although there is little indication of any specific pattern to these differences. It is of interest, however, that arch width at the canines and molars has a larger coefficient of variation in the lower arch than in the upper arch in both sexes.

Age changes.

The cross-sectional age changes for all variables are presented in Tables 6 and 7 for males and females, respectively. For each variable, the linear

Table 4

Incidence of Selected Occlusal Anomalies

Variable	Males (N=319)		Females (N=359)		Total (N=678)	
	N	%	N	%	N	%
Maxillary Midline Diastema	31	9.7	59	16.4	90	13.3
Posterior Cross-bite (buccal)	15	4.7	5	1.4	20	2.9
Posterior Cross-bite (lingual)	30	9.4	19	5.3	49	7.2
Canine Openbite (right or left)	6	1.9	22	6.1	28	4.1
Posterior Openbite (right or left)	9	2.8	16	4.5	25	3.7

Table 5
Incidence of Types of Occlusion by Angle's Classification

Class	Males (N=319)		Females (N=359)		Total (N=678)	
	N	%	N	%	N	%
Ideal Occlusion	101	31.7	119	33.1	220	32.5
Class I malocclusion	168	52.7	176	49.0	344	50.7
Class II Division 1	33	10.3	47	13.1	80	11.8
Class II Division 2	9	2.8	12	3.3	21	3.1
Class III	8	2.5	5	1.4	13	1.9

product-moment correlation coefficient, the coefficients of the best fitting polynomial regression equation, and the R^2 and F ratio for this equation are given.

The large number of independent statistical tests used in the calculation of the total group of age-changes would lead to an expectation of some spuriously significant results. One evaluation of this problem can be made through the comparison of findings for males and females. With little basis for expecting differences between the sexes in the post-pubertal pattern of changes with age, significant results for one sex only would be suspect. However, little evidence of this problem was found, only two variables, the sagittal molar relationship and anterior overbite-openbite having a significant regression in one sex (males) but not in the other. This may be related to the observations of Paulsen (71) that between 12 and 20 years of age there is greater mandibular growth and change in the molar relationship in males than in females.

All other occlusal variables and arch measurements exhibited similar patterns in both sexes. There is an increase in crowding and malalignment with age in both the maxillary and mandibular arches. The negative slope for crowding-spacing must be interpreted with the scoring system in mind. Low values, and therefore a negative slope, indicate crowding, while high values and a positive slope would indicate spacing. The remaining occlusal variable, overjet, apparently has no age-related variance in this population.

The regressions for the length and width of the dental arches and their ratios are all highly significant. Length of the upper and lower arches decrease with age in both sexes with little deviation from linearity. One explanation for this change may be interproximal attrition. The slope of approximately 0.03 would indicate a total of 1.5 mm of attrition over 50

Age Changes in Occlusal Variables and Arch Measurements (Males)^a

Variable ^b	Linear Correlation with age	Coefficients of best-fitting regression equation				R ²	F ratio ^c
		Constant	Linear	Quadratic	Cubic		
Molar relationship ^d	+.10	1.45	.067	-.00092		.03	3.50*
Overjet ^d	-.11	2.95	-.012			.01	2.89
Anterior overbite- openbite	-.17	4.35	-.12	.0016		.05	6.82**
Upper anterior crowding-spacing	-.30	3.61	-.34	.0086	-.00007	.14	13.40**
Lower anterior crowding-spacing	-.34	0.84	-.088	.00098		.14	19.71**
Upper rotations and displacements	+.22	0.56	.028			.05	12.28**
Lower rotations and displacements	+.32	0.77	.049			.10	28.07**
Upper canine arch width	-.18	42.79	-.032			.03	8.46**
Upper molar arch width	+.24	52.76	.75	-.018	.00014	.13	11.94**
Lower canine arch width	-.19	33.37	-.027			.03	8.66**
Lower molar arch width	+.23	52.04	.31	-.0041		.13	18.19**
Upper arch length ^d	-.20	48.29	-.032			.04	9.99**
Lower arch length ^d	-.19	43.91	-.026			.03	8.66**
Upper arch shape	-.39	91.76	-1.19	.028	-.00020	.25	26.69**
Lower arch shape	-.37	85.13	-.56	.0071		.24	38.14**
Upper width ratio	-.43	81.97	-1.15	.028	-.00021	.28	31.60**
Lower width ratio	-.37	63.30	-.33	.0038		.18	25.98**

* p < .05 ** p < .01

^a N = 242^b All variables in mm. except anterior crowding-spacing, rotation and displacement scores and arch width and shape ratios. See measurement definitions for these scales.^c Regression MS (of best-fitting polynomial regression) ÷ Residual MS^d Mean value of left and right sides

Table 7

Age Changes in Occlusal Variables and Arch Measurements (Females)^a

Variable ^b	Linear Correlation with age	Coefficients of best-fitting regression equation				R ²	F Ratio ^c
		Constant	Linear	Quadratic	Cubic		
Molar relationship ^d	+ .05	2.04	.0044			.002	0.68
Overjet ^d	- .04	2.61	-.0033			.001	0.35
Anterior overbite- openbite	- .12	2.98	-.014			.01	3.84
Upper anterior crowding-spacing	- .33	2.11	-.13	.0016		.15	24.59**
Lower anterior crowding-spacing	- .37	0.91	-.084	.00077		.15	24.70**
Upper rotations and displacements	+ .23	0.52	.031			.05	15.31**
Lower rotations and displacements	+ .21	-0.15	.13	-.0015		.06	8.66**
Upper canine arch width	- .14	41.56	-.026			.02	5.80*
Upper molar arch width	+ .15	58.08	.032			.02	6.24*
Lower canine arch width	- .32	32.87	-.055			.10	30.88**
Lower molar arch width	+ .16	53.73	.034			.03	7.60**
Upper arch length ^d	- .21	48.15	-.13	.0015		.06	8.93**
Lower arch length ^d	- .19	42.93	-.029			.04	10.18**
Upper arch shape	- .36	80.69	-.10			.13	40.61**
Lower arch shape	- .34	79.89	-.10			.12	36.24**
Upper width ratio	- .32	71.55	-.081			.10	31.77**
Lower width ratio	- .47	63.23	-.29	.0025		.24	42.91**

* p < .05 ** p < .01

a N=279

b All variables in mm. except anterior crowding-spacing, rotation and displacement scores and arch width and shape ratios. See measurement definitions for these scales.

c Regression MS (of best-fitting polynomial regression) ÷ Residual MS

d Mean value of left and right sides.

years on each side of the upper and lower arches.

Canine arch width also decreases linearly with age in the upper and lower arches of both sexes. As with arch length, interproximal attrition and forward drift may account for these changes. Maxillary and mandibular molar arch widths, however, increase with age. In males, there is also a highly significant deviation from linearity. The cubic trend in the maxillary arch suggests that width increases in the male population up to about 30 years of age and then remains relatively constant (Table 6, Fig. 1). As a result of these changes, the arch width ratios and arch shape ratios also undergo significant alterations (Tables 6,7; Figs. 2,3).

The data were also examined for changes in the magnitude of variation across age groups. When grouped by 10 year age intervals, there appears to be some tendency for the older age groups to be more variable for most characteristics in the female sample (Table 8). This was not apparent for the male population.

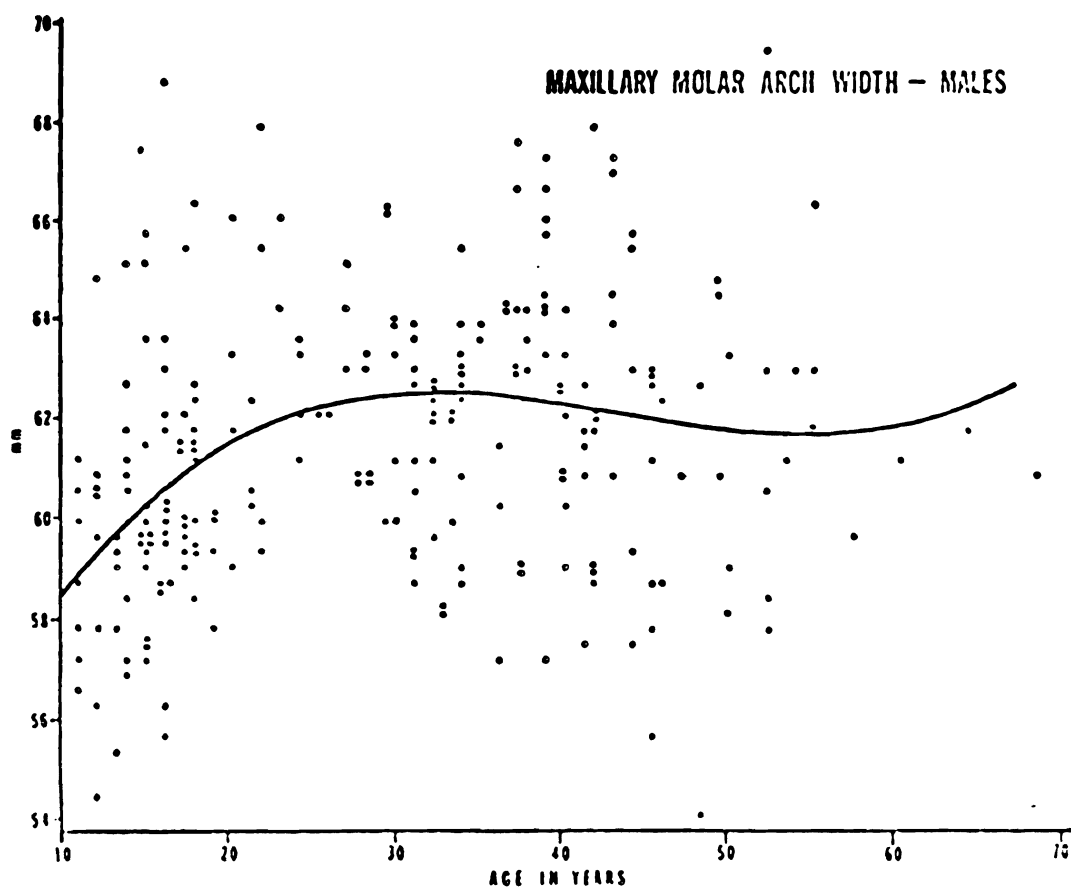


Figure 1

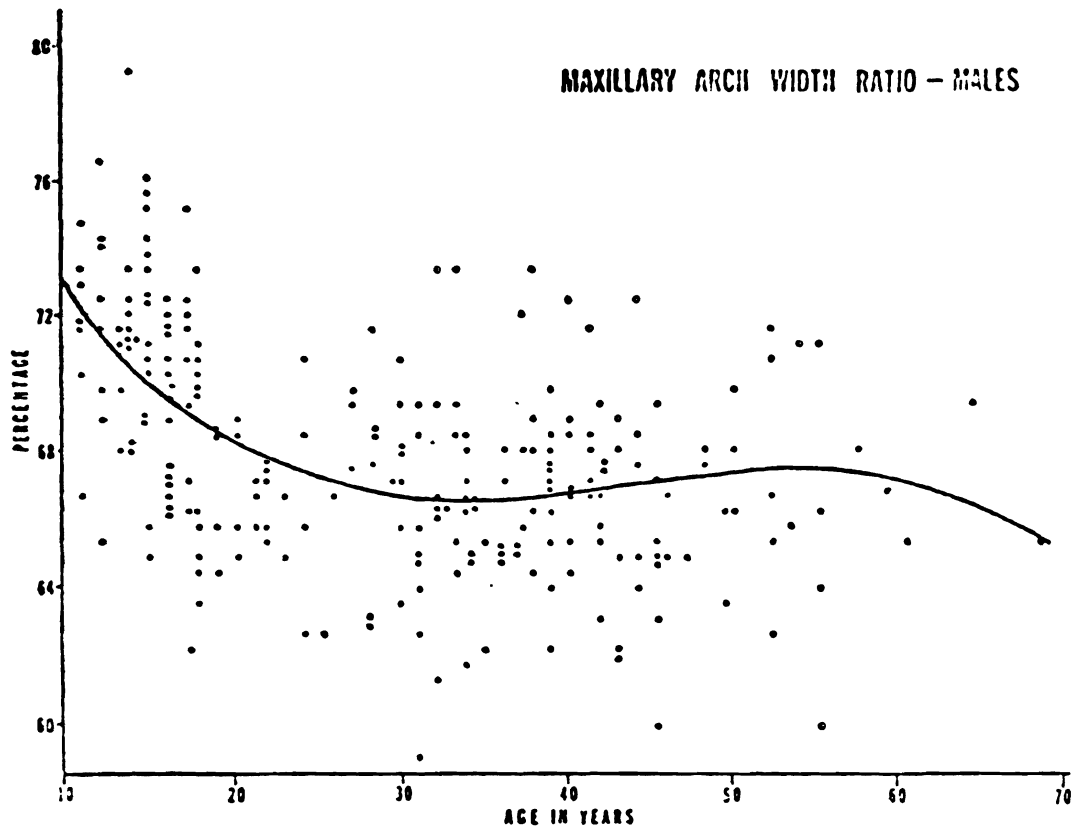


Figure 2

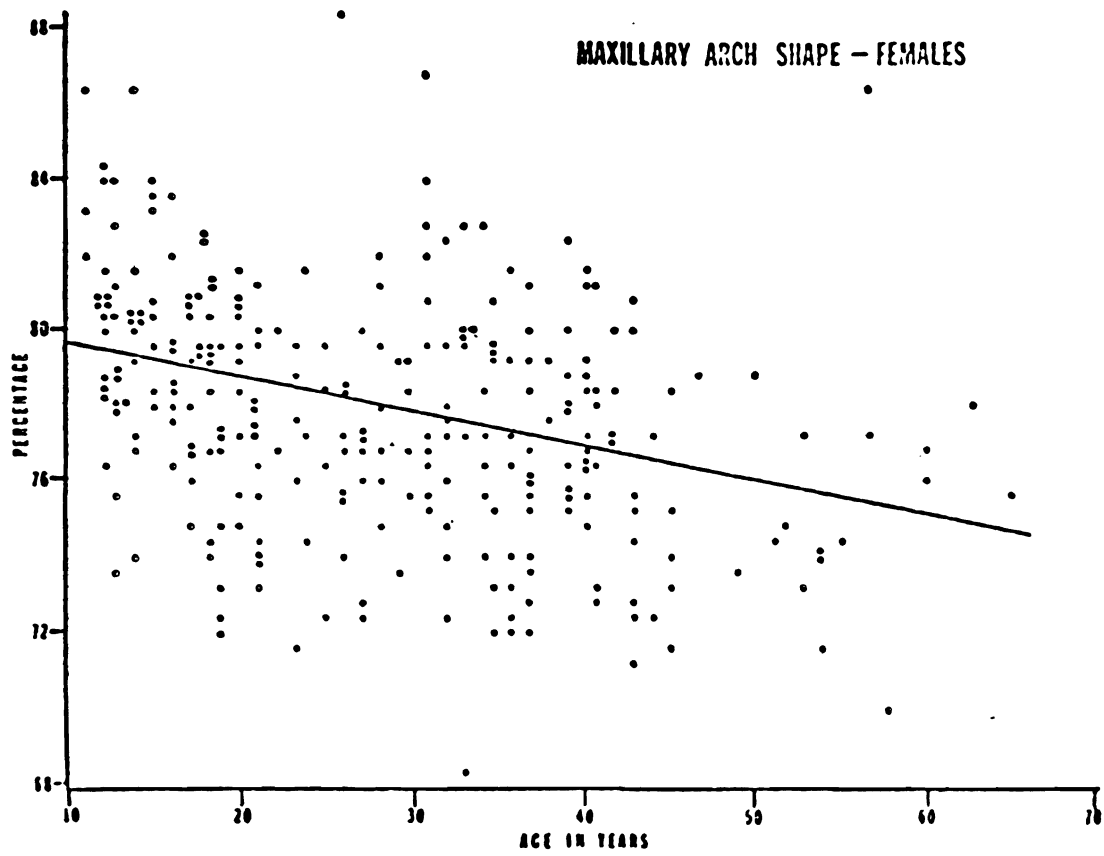


Figure 3

Table 8
Changes in Variation by Age (Females)

Molar relationship S.D.	Overjet S.D.	Overbite S.D.	Upper Canine Width C.V.	Upper Molar Width C.V.	Lower Canine Width C.V.	Lower Molar Width C.V.	Upper Arch Length C.V.
.91	.78	1.3	4.6	3.8	4.3	4.0	4.1
1.0	.93	1.3	4.3	3.9	5.6	3.8	3.6
1.1	1.2	1.5	5.3	4.8	7.2	4.9	4.0
1.3	1.6	1.7	6.6	5.3	9.4	5.8	4.6
1.3	1.1	1.7	7.7	5.1	6.7	5.1	4.4

Standard deviation. C.V., coefficient of variation.

DISCUSSION

Sex differences.

As recently reviewed by Jago (74) few sex differences in dental occlusion have been consistently observed. The greater width and length of the dental arches of males was expected and reflects the general sex dimorphism in body size.

Although small in magnitude, several other sex differences were similar to those observed by Lombardi and Bailit (72) for another Melanesian group, the Kwaio of Malaita. Both reports observed greater overjet and lower incisor crowding in males, and more posterior openbite in females. This latter observation may be due to the custom of pipe-smoking which is common to all adults in these populations but more vigorously pursued by women (Lombardi and Bailit, 72). In total, however, the results emphasize that human variation in dental occlusion is not highly related to any systematic differences between the sexes.

Age changes.

Given the cross-sectional data of the present investigation, a conclusive distinction cannot be made between (1) a longitudinal age change, (2) an environmental secular effect, (3) an effect due to gene flow, or (4) directional genetic selection. With analysis limited to subjects with complete permanent dentitions, it is also possible that these changes only represent a bias introduced by sample selection, i.e., the results indicate those individuals most likely to retain their permanent teeth with increasing age.

However, most observations are in the direction expected for individual longitudinal age effects. The anterior segments became more crowded and both the intercanine widths and arch lengths decreased with increasing age. Several

factors may be responsible for these interrelated trends. In addition to lingual uprighing of incisors as a late growth change (Siatkowski, 74), molars and premolars erupt along a mesial inclination (Bjork and Skeiller, 72) during growth and in compensation for attrition of the occlusal surface. Wolpoff (71) has reviewed the concept of a mesial vector of force resulting from the direction of occlusal forces in relation to the long axes of the teeth. Biomechanically, however, this hypothesis remains problematical. No model for this mesial force vector has yet incorporated the tipping tendency (i.e., moment) that would result from the vertical forces of occlusion passing anterior to the center of resistance of mesially inclined teeth. The presence of a curve of Spee or a bolus of food during mastication would also have substantial effects on the direction of occlusal forces. In addition, our results do not confirm the expectation under this model that the lower arch would demonstrate a greater reduction in length than the upper arch (Wolpoff, 71).

The upper and lower arch width at the first molars increased in both sexes with age. Until approximately 17 years of age, this increase probably reflects the wedge-shaped growth occurring at the midpalatal suture, which increases in width more posteriorly than anteriorly (Bjork and Skieller, 74). It appears, however, that intermolar width continues to increase beyond the completion of sutural growth. Enlargement of other cranial dimensions beyond 30 years of age has been confirmed by others (Kendrick and Risinger, 67; Israel, 73). Appositional bone deposition on the lateral borders of the alveolus and lateral drift of the teeth seems a possible explanation, although Bjork and Skieller (74) emphasize that little is known about appositional growth of maxillary alveolar width, and Enlow (68) has demonstrated that simple apposition cannot occur without sutural involvement and

considerable remodeling to maintain shape relationships.

In general, even though many of the regressions with age were statistically significant, the total variance accounted for by age for each variable was small and of little value in prediction or in explaining the range of variation within Bougainville. Using 0.1 mm as a typical standard error of measurement and 0.03 mm/year as an average slope for the width and length changes, the age change predicted over a 10 year period would not fall outside of the 95% confidence interval of an individual measurement.

For this reason, and because the age changes were similar in both sexes, no adjustment for age was made in calculating mean values for each characteristic (Tables 2,3) or for testing sex differences. However, subjects with known ages were compared for sex differences after eliminating all age-related variance by making a correction based upon the highest degree significant polynomial for each variable. The resulting relationships differed minimally in magnitude from those based upon raw scores and had no effect on relative relationships among variables.

Variation among populations.

Comparisons of population means for occlusal variables between this sample and other studies are of limited value because of the lack of consistent measurement definitions and techniques among investigators. However, because of the large amount of data available on Angle's classification, some general trends with this variable do emerge. The low frequency of 1 to 2% Class III occlusions in this sample confirms the observations of Lombardi and Bailit (72) for another Melanesian group. This distinguishes Melanesians and Australian aborigines (Clinch, 51) from the Polynesians of Pukapuku, with a reported incidence of 14% Class III occlusions (Davies, 56). The high incidence of Class III relationships in Polynesia has also been observed by Baume (74) and is similar to the frequency reported for Alaskan Eskimos (Wood, 71),

Aleuts (Moorrees, 57) and American Indians (Foster, 42). This division of Oceanic peoples into two groups - Australian aborigines and Melanesians in one and Aleuts, Eskimos, Polynesians and American Indians in the other - is similar to that suggested by Riesenfeld (56) on the basis of other dental traits, and may be of some relevance to the complex problems of Oceanic prehistory (Howells, 73).

Although only limited observations can be made about differences among populations in mean values, more extensive evaluations are possible regarding population differences in variability, since the addition or subtraction of a constant value from each individual due to investigator biases should not effect measures of variation. To provide comparative data for this purpose, the literature was searched for quantitative studies of dental occlusion from which relatively unbiased estimates of population variation could be obtained. Selection of studies was limited to those which restricted age to a maximum of a ten year interval between 13 and 35 years of age, reported results separately by sex, and provided sufficient data to calculate all basic descriptive statistics.

The age restriction was made to eliminate effects due to differing population pyramids on variables which changes with age. Although this was not important for the Bougainville population, other groups may exhibit more significant age-related effects. Accordingly, for consistency, only two subgroups of the Bougainville population were used in the analysis, those 15 to 19 and those 20 to 29 years of age. The results, shown in Figs. 4 to 9, are for the male samples only. Similar results were obtained for females on all variables. The coefficient of variation is used in these comparisons, except for variables with negative values contributing to the calculation of the mean, in which case comparisons are based directly on the standard

deviation. Since slightly differing measurement definitions were used in some studies, the results should best be interpreted as indicative of general trends, rather than as specific comparisons of any two or more populations.²

The observations indicate that the different variables fall into one of three general categories when the magnitude of variation on Bougainville is compared to industrialized populations. Maxillary arch length (Fig. 4) and maxillary arch width at the molars (Fig. 5) appear to be moderately less variable in the Bougainville population. Similar results were found for the corresponding measurements in the mandibular arch. As reviewed by Niswander et al. (67), some reduction in variability is expected, since the environment is relatively homogeneous and the necessary inclusion of related individuals decreases genetic variance.

One variable, the sagittal molar relationship (Fig. 6), is much less variable in Bougainville. Other workers have reported an increased occurrence of malocclusion following industrialization (Price, 35; Niswander, 67), and these observations suggest that the environmental factors responsible may be specifically related to the sagittal jaw relationship. It is interesting in this regard that in two independent studies of industrialized groups, Lundstrom (48) and Chung and Niswander (75) found the molar relationship to be the least heritable of all the arch size, tooth size and occlusal variables examined. This indicates that in proportion to the amount of genetic variance, the environmental variance was greater than that for any other trait. It is also likely that the industrialized groups are more variable because of drift of molars following tooth loss.

The remaining three variables, maxillary canine arch width (Fig. 7), anterior overbite - openbite (Fig. 8) and overjet (Fig. 9), have similar variability in all groups. The maintenance of a large amount of phenotypic

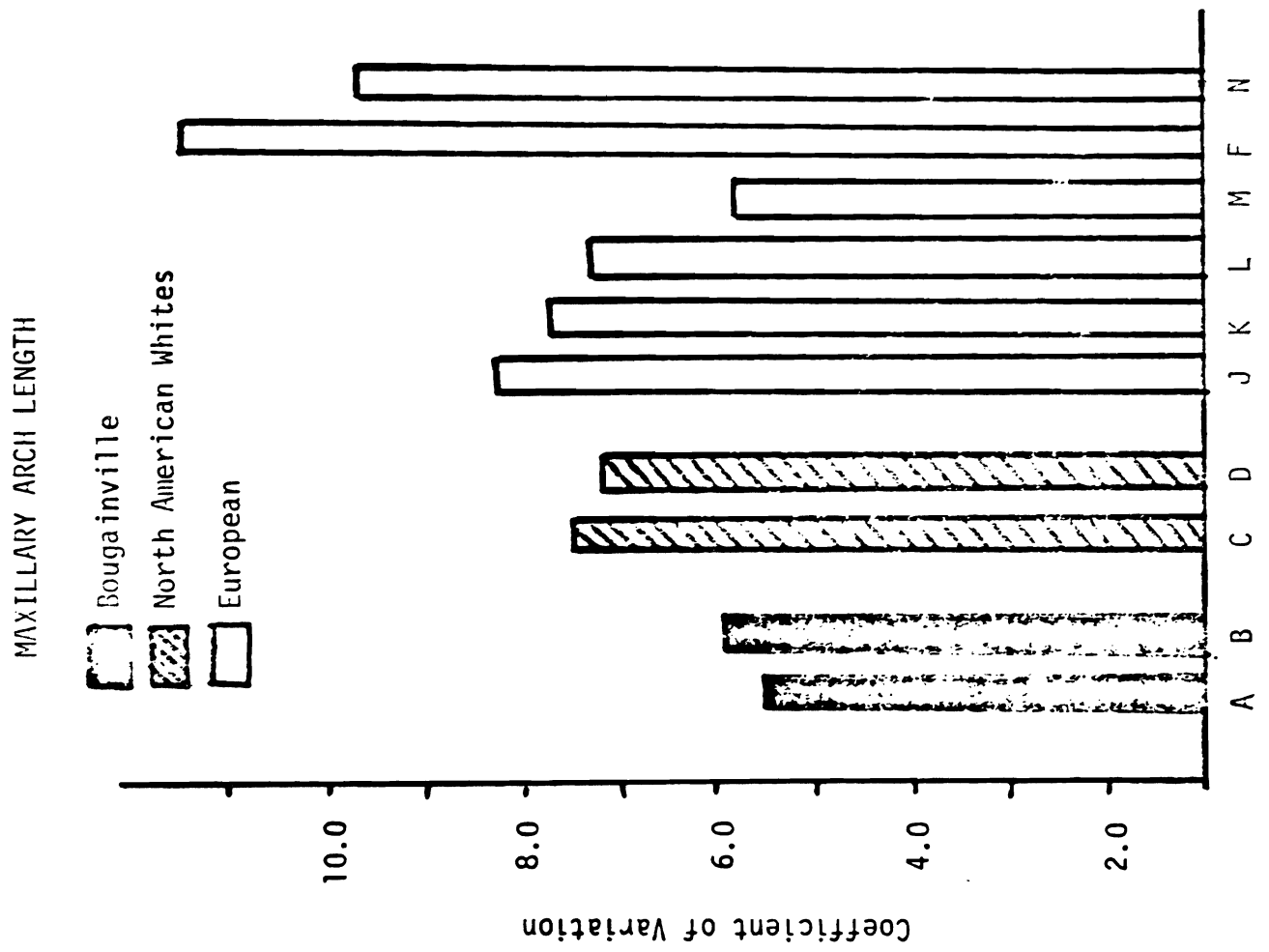


Figure 4

MAXILLARY MOLAR ARCH WIDTH

Bougainville

North American Whites

European

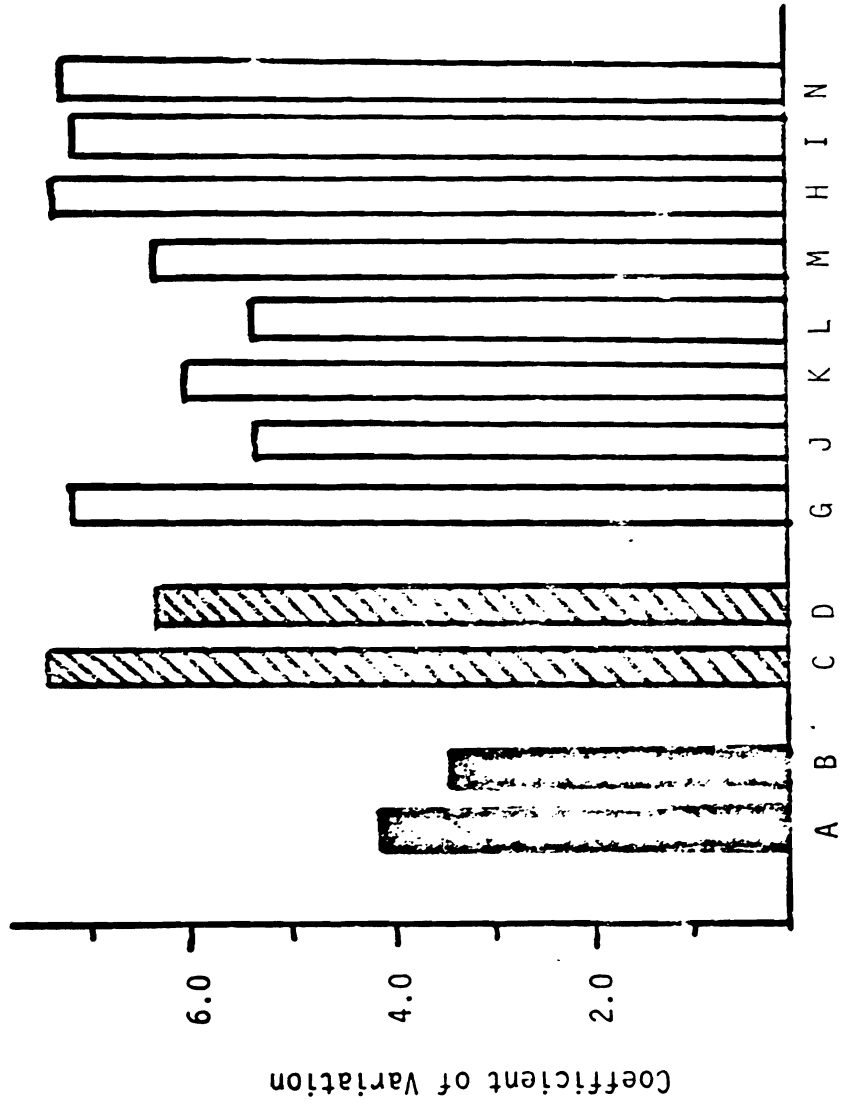
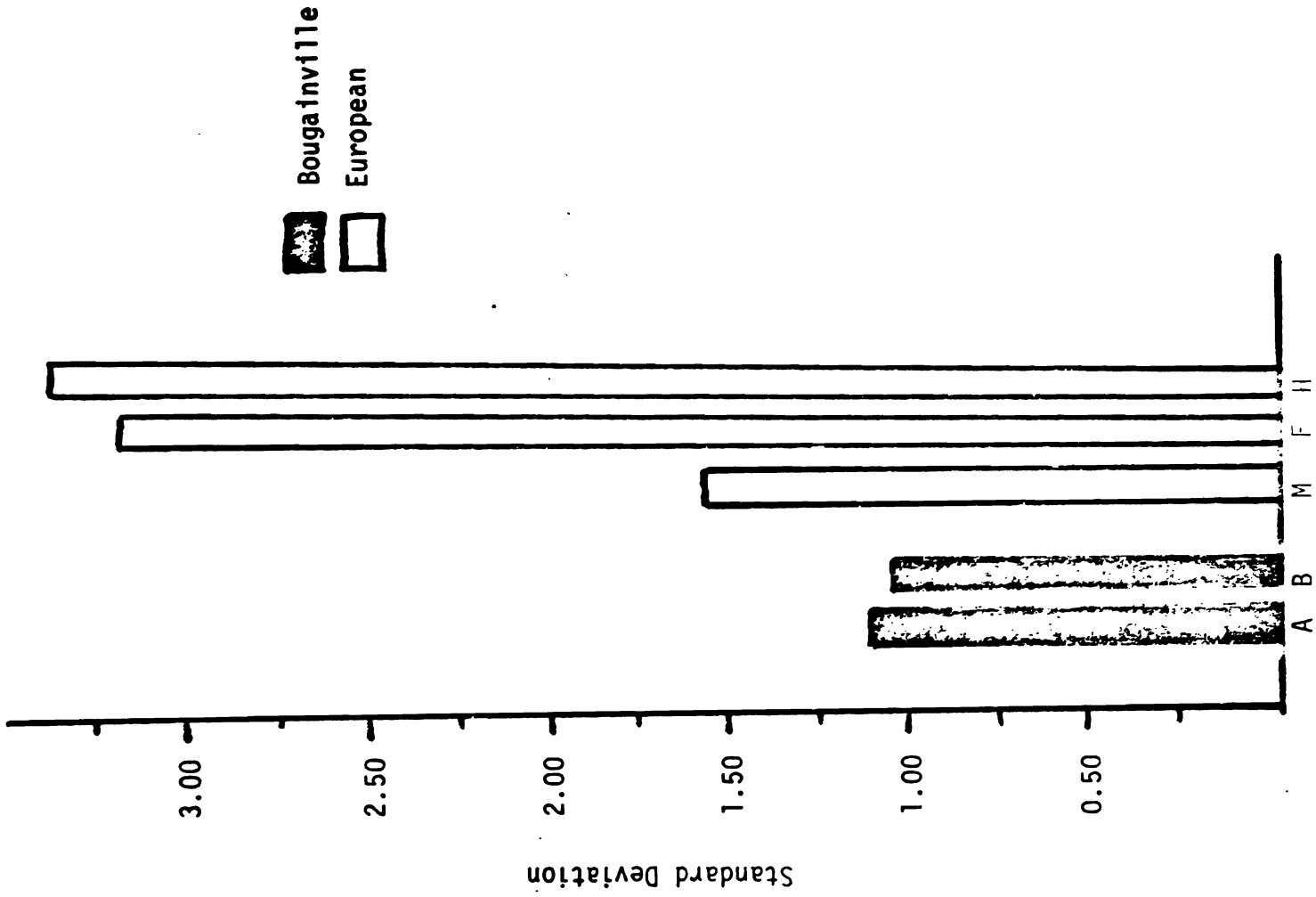


Figure 5

SAGITTAL MOLAR RELATIONSHIP



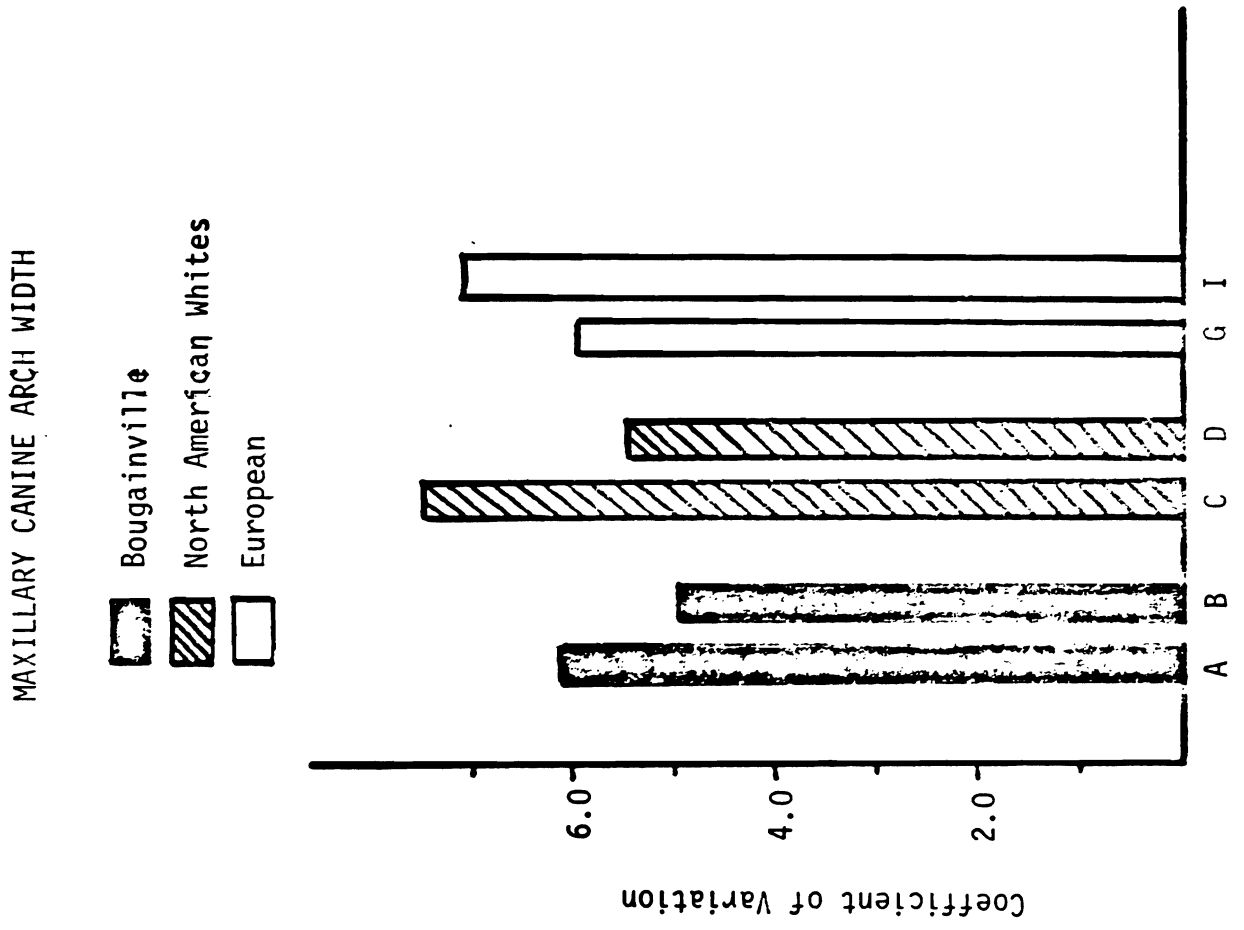


Figure 7

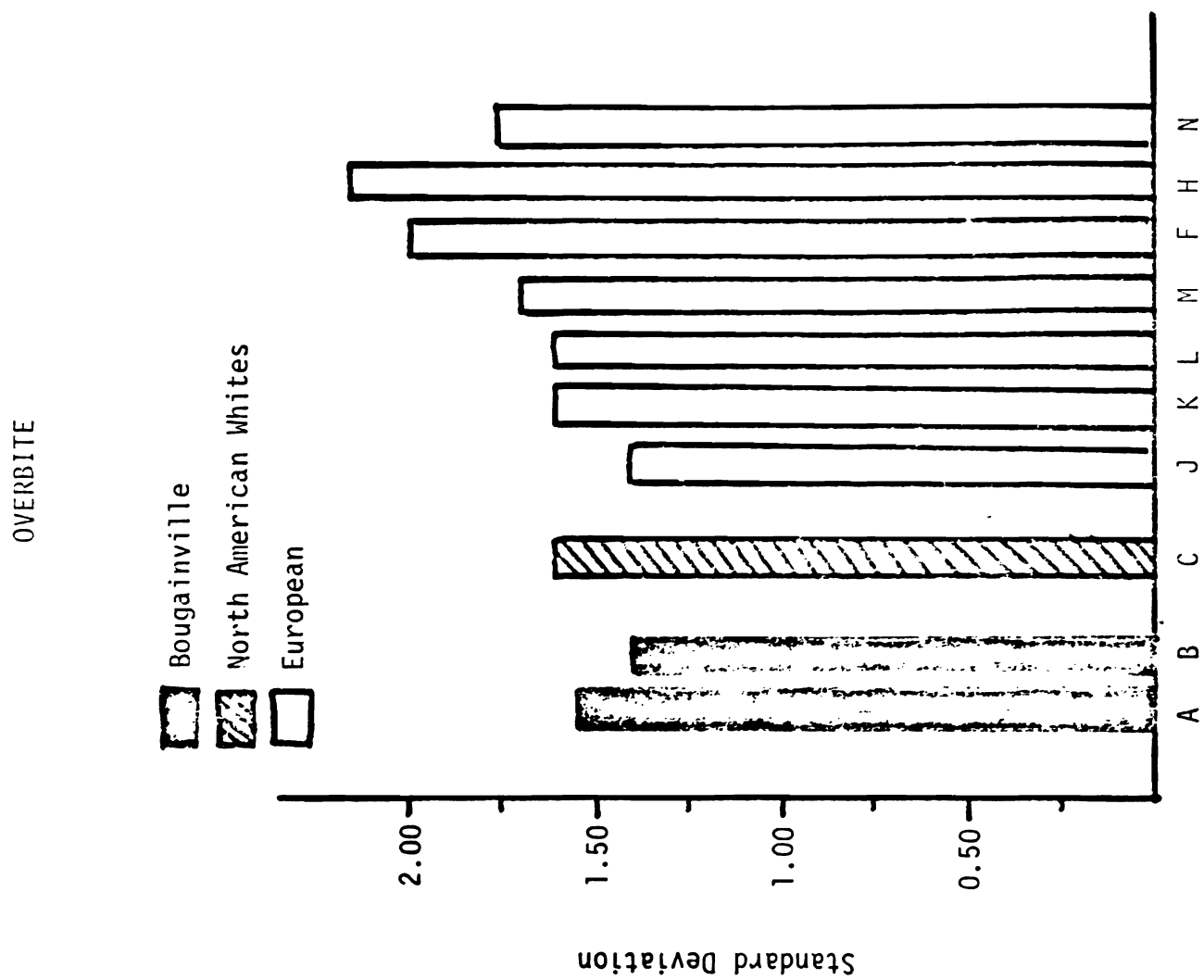


Figure 8

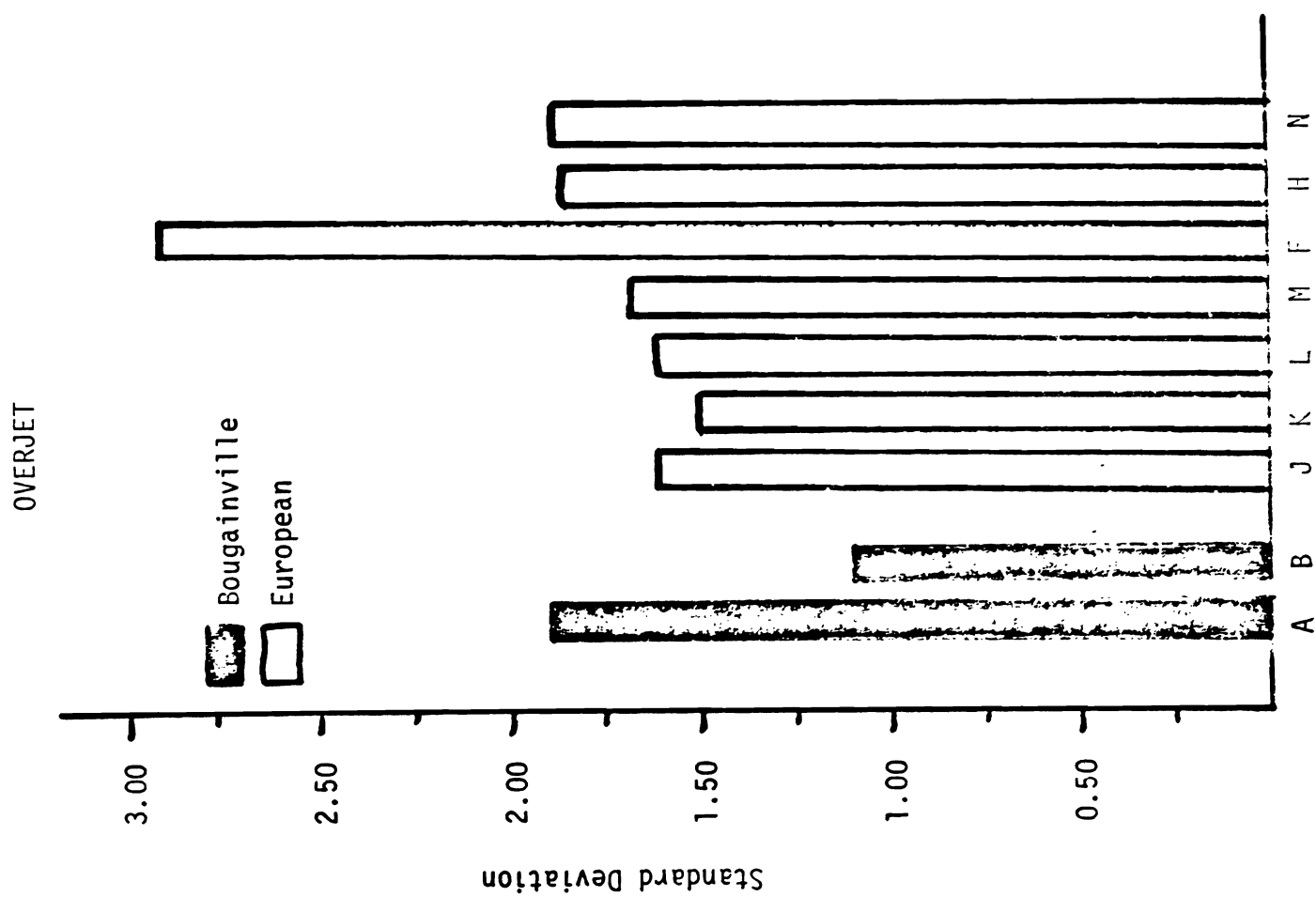


Figure 9

variation when there are reasons to expect a decrease in both environmental and genetic variance cannot be satisfactorily explained. One mechanism would be decreased developmental homeostasis (buffering or canalization) (Lerner, 54) because of increased homozygosity following inbreeding. However, Bailit et al. (68a) reviewed this possibility when they found increased variability in tooth size within one language group on Bougainville, and concluded that it was an unlikely explanation.

In conclusion, these data have demonstrated that the concept of interval scale, continuous variation is of value in the analysis of dental occlusion. This approach provides more information and rests upon sounder biologic principles than does the study of "malocclusion" frequencies.

Additional research with this orientation is needed on other human populations, so that diet, ethnicity, climate, age, sex and other factors can be evaluated for their contributions to the observed variation. Patterns of microdifferentiation and clinal variation have been considered in only limited respects (Guttman et al., 67; Boyd, 72), and a more extensive evaluation of these parameters is in progress on the Bougainville population. Perhaps most importantly, however, a quantitative approach to dental occlusion needs to be applied in family studies, since phenotypic data in general are of limited value in making taxonomic distinctions or in evaluating evolutionary change when the genotypic basis for the characteristics in question is entirely unknown.

FOOTNOTES

- ¹ Nupatoro, Okowopaia, Kopani, Kopikiri, Nasiwoiwa, Atamo, Uruto, Karnavitu, Boira, Korpei, Pomaua and Bairima (see Friedlaender, 75).
- ² Studies are identified in the figures by letter, as follows: A, Bougainville males, 15-19 years of age; B, Bougainville males, 20-29 years of age; C, Moorrees (59); D, Sillman (64); E, Anderson and Thompson (73); F, Bjork (47); G, Bjork (64); H, Seipel (46); I, Olow (54); J, Lundstrom (53) Swedish subjects; K, Lundstrom (53) Greek subjects; L, Lundstrom (53) Turkish subjects; M, Solow (66); N, Ingervall et al. (72).

FIGURE LEGENDS

Figure 1. Cross-sectional age changes in maxillary arch width at the first molars for males. The cubic equation $y = 52.76 + 0.75x - 0.018x^2 + 0.00014x^3$ accounts for 13% of the variance.

Figure 2. Cross-sectional age changes in the maxillary arch width ratio for males. The cubic equation $y = 81.97 - 1.15x + 0.028x^2 - 0.00021x^3$ accounts for 28% of the variance.

Figure 3. Cross-sectional age changes in maxillary arch shape for females. The linear equation $y = 80.69 - 0.10x$ accounts for 13% of the variance.

Figure 4. A comparison among populations in variability of maxillary arch length. There is a moderately reduced amount of variation on Bougainville compared with industrialized populations.

Figure 5. A comparison among populations in variability of maxillary arch width at the first molars. There is a moderately reduced amount of variation on Bougainville compared with industrialized populations.

Figure 6. A comparison among populations in variability of the sagittal molar relationship. There is a marked reduction in the magnitude of variation on Bougainville compared with industrialized populations.

Figure 7. A comparison among populations in variability of maxillary arch width at the canines. The Bougainville males appear to be approximately as variable as the industrialized populations.

Figure 8. A comparison among populations in variability of anterior overbite-openbite. The Bougainville males appear to be approximately as variable as the industrialized populations.

Figure 9. A comparison among populations in variability of overjet.

The Bougainville males appear to be approximately as variable as the industrialized populations.

LITERATURE CITED

- Anderson, D.L. and G.W. Thompson 1973 Interrelationships and sex differences of dental and skeletal measurements. J. Dent. Res. 52: 431-438.
- Angle, E.H. 1899 Classification of malocclusion. Dent. Cosmos 41: 248-264, 350-357.
- Bailit, H.L., S.J. DeWitt and R.A. Leigh 1968a The size and morphology of the Nasioi dentition. Am. J. Phys. Anthropol. 28: 271-288.
- Bailit, H.L., E. Ogan and R. Leigh 1968b Oral health of the Nasioi of Bougainville. Aust. Dent. J. 13: 353-359.
- Baume, L.J. 1974 Uniform methods for the epidemiologic assessment of malocclusion. Results obtained with the World Health Organization standard methods (1962 and 1971) in South Pacific populations. Am. J. Orthodont. 66: 251-272.
- Baume, L.J., H.S. Horowitz, C.J. Summers, O. Backer Dirks, W.A.B. Brown, J.P. Carlos, L.K. Cohen, T.J. Freer, E.P. Harvold, C.F.A. Moorrees, J.A. Salzmann, G. Schmuth, B. Solow and H. Taatz 1973 A method for measuring occlusal traits. Int. Dent. J. 23: 530-537.
- Bjork, A. 1947 The face in profile. Svensk Tandlak T. 40: Suppl.
- Bjork, A. cited by Beyron, H. 1964 Occlusal relations and mastication in Australian aborigines. Acta Odont. Scand. 22: 597-678.
- Bjork, A. and V. Skieller 1972 Facial development and tooth eruption. Amer. J. Orthodont. 62: 339-383.
- Bjork, A. and V. Skieller 1974 Growth in width of the maxilla studied by the implant method. Scand. J. Plast. Reconstr. Surg. 8: 26-33.
- Boyd, R.C. 1972 An odontometric and observational assessment of the dentition. In Littlewood, R.A.: Physical Anthropology of the Eastern Highlands of New Guinea. Univ. Washington Press, Seattle.
- Chung, C.S. and J.D. Niswander 1975 Genetic and epidemiologic studies of oral characteristics in Hawaii's schoolchildren. V. Sibling correlations in occlusal traits. J. Dent. Res. 54: 324-329.
- Churchill, E. 1963 The modern computer and physical anthropology. Am. J. Phys. Anthropol. 21: 426.
- Clinch, L. 1951 The occlusion of the Australian aborigine. Trans. Europ. Orthodont. Soc. 80-93.
- Damon, A. 1973 Some genetic traits in Solomon Island populations. I. Introduction: people and habitats. Am. J. Phys. Anthropol. 39: 169-178.

- Davies, G.N. 1956 Dental conditions among the Polynesians of Pukapuka (Danger Island). I. General background and the prevalence of malocclusion. J. Dent. Res. 35: 115-131.
- Enlow, D.H. 1968 The Human Face. Harper and Row, New York.
- Foster, L.W. 1942 Dental conditions in White and Indian children of northern Wisconsin. J. Am. Dent. Assoc. 29: 2251-2255.
- Friedlaender, J.S. 1969 Biological Diversity over Population Boundaries in South-Central Bougainville. Unpublished Ph.D. thesis, Harvard University, Cambridge, Mass.
- Friedlaender, J.S. 1971 Isolation by distance in Bougainville. Proc. Nat. Acad. Sci, U.S.A. 68: 704-707.
- Friedlaender, J.S. 1975 Patterns of Human Variation. The Demography, Genetics and Phenetics of Bougainville Islanders. Cambridge: Harvard Univ. Press.
- Friedlaender, J.S., L.A. Sgaramella-Zonta, K.K. Kidd, L.Y.C. Lai, P. Clark and R.J. Walsh 1971 Biological divergences in south-central Bougainville: An analysis of blood polymorphism gene frequencies and anthropometric measurements utilizing tree models, and a comparison of these variables with linguistic, geographic, and migrational "distances." Am. J. Hum. Genet. 23: 253-270.
- Guttman, R., L. Guttman and K.A. Rosenzweig 1967 Cross-ethnic variation in dental, sensory and perceptual traits: a nonmetric multibivariate derivation of distances for ethnic groups and traits. Amer. J. Phys. Anthropol. 27: 259-276.
- Helm, S. 1968 Malocclusion in Danish children with adolescent dentitions. An epidemiologic study. Am. J. Orthodont. 54: 352-368.
- Howells, W.W. 1973 The Pacific Islanders. New York: Charles Scribner's Sons.
- Ingervall, B., T. Lewin and B. Hedegard 1972 Secular changes in the morphology of the skull in Swedish men. Acta Odont. Scand. 30: 539-554.
- Israel, H. 1973 Age factor and the pattern of change in craniofacial structures. Am. J. Phys. Anthropol. 39: 111-128.
- Jago, J.D. 1974 The epidemiology of dental occlusion; a critical appraisal. J. Pub. Health Dent. 34: 80-93.
- Keith, A. 1924 Concerning certain structural changes which are taking place in our jaws and teeth. In: The Growth of the Jaws, Normal and Abnormal, in Health and Disease. London: Dental Board of the United Kingdom.
- Kendrick, G.S. and H.L. Risinger 1967 Changes in the anteroposterior dimensions of the human male skull during the third and fourth decades of life. Anat. Rec. 159: 77-81.

- Kerlinger, F.N. and E.J. Pedhazur 1973 Multiple Regression in Behavioral Research. New York: Holt, Rinehart and Winston.
- Knott, V.B. 1961 Size and form of dental arches in children with good occlusion: studied longitudinally from age 9 years to late adolescence. Am. J. Phys. Anthropol. 19: 263-284.
- Lerner, I.M. 1954 Genetic Homeostasis. John Wiley & Sons, Inc. New York
- Lombardi, A.V. and H.L. Bailit 1972 Malocclusion in the Kwaio, a Melanesian group on Malaita, Solomon Islands. Am. J. Phys. Anthropol. 36: 283-294.
- Lundstrom, A. 1948 Tooth Size and Occlusion in Twins. New York: S. Karger.
- Lundstrom, A. 1953 An anthropological comparison of the dentitions of 71 Greek, 69 Turkish and 140 Swedish boys of about 13 years of age. Acta Genet. 4: 247-257.
- Meredith, H.V. and G.C. Cox 1954 Width of the dental arches at the permanent first molars in children 9 years of age. Am. J. Orthodont. 40: 134-144.
- Moorrees, C.F.A. 1957 The Aleut Dentition. Cambridge: Harvard Univ Press
- Moorrees, C.F.A. 1959 The Dentition of the Growing Child. Cambridge: Harvard Univ. Press.
- Moorrees, C.F.A. and R.R. Reed 1954 Biometrics of crowding and spacing of the teeth in the mandible. Am. J. Phys. Anthropol. 12: 77-88.
- Nie, N.H., D.H. Bent and C.H. Hull 1970 Statistical Package for the Social Sciences. New York: McGraw-Hill Book Co.
- Niswander, J.D. 1967 Further studies on the Xavante Indians. VII. The oral status of the Xavantes of Simoes Lopes. Am. J. Hum. Genet. 19: 543-553.
- Niswander, J.D., F. Keiter and J.V. Neel 1967 Further studies on the Xavante Indians. II. Some anthropometric, dermatoglyphic, and non-quantitative morphological traits of the Xavantes of Simoes Lopes. Am. J. Hum. Genet. 19: 490-501.
- Oliver, D.L. 1955 A Solomon Island Society. Boston: Beacon Press
- Olow, M. 1954 A metric study of transversal size of the dental arches in children at 7, 12 and 18 years of age. Odont. Tidsk. 62: 266-297.
- Paulsen, H.U. 1971 Changes in sagittal molar occlusion during growth. Tandlaegebladet 75: 1258-1267.
- Price, W.A. 1935 Studies of relationships between nutritional deficiencies and (a) facial and dental arch deformities and (b) loss of immunity to dental caries among South Sea Islanders and Florida Indians. Dent. Cosmos 77: 1033-1045.

- Riesenfeld, A. 1956 Shovel-shaped incisors and a few other dental features among the native peoples of the Pacific. Am. J. Phys. Anthropol. 14: 505-521.
- Seipel, C.M. 1946 Variation of tooth position. Svensk Tandlaek. Tidskr. 39: Suppl.
- Siatkowski, R.E. 1974 Incisor uprighting: mechanism for late secondary crowding in the anterior segments of the dental arches. Amer. J. Orthodont. 66: 398-410.
- Sillman, J.H. 1964 Dimensional changes of the dental arches: longitudinal study from birth to 25 years. Amer. J. Orthodont. 50: 824-842.
- Simons, E.L. and D.R. Pilbeam 1965 Preliminary revision of the Dryopithecinae (Pongidae, Anthropoidea). Folia Primat. 3: 81-152.
- Smith, R.J. and H.L. Bailit 1976 Problems and methods in research on the genetics of dental occlusion. Angle Orthodont. In Press
- Sokal, R.R. and F.J. Rohlf 1969 Biometry. W.H. Freeman and Co., San Francisco.
- Solow, B. 1966 The pattern of craniofacial associations. Acta Odont. Scand. 24: Suppl. 46.
- Summers, C.J. 1971 The occlusal index: a system for identifying and scoring occlusal disorders. Am. J. Orthodont. 59: 552-567.
- Walker, A. and P. Andrews 1973 Reconstruction of the dental arcades of Ramapithecus wickeri. Nature 244: 313-14.
- Wolpoff, M.H. 1971 Interstitial wear. Am. J. Phys. Anthropol. 34: 205-228.
- Wood, B.F. 1971 Malocclusion in the modern Alaskan Eskimo. Am. J. Orthodont. 60: 344-354.

Part III

**Variation in Dental Occlusion and Arches among Melanesians of
Bougainville Island, Papua New Guinea.**

II. Clinal Variation, Geographic Microdifferentiation and Synthesis.

Some preliminary studies (Guttmann et al., et al., '67; Boyd, '72) suggest that dental occlusion and the size and shape of the dental arches may be useful for differentiating among populations at a microevolutionary level. The purpose of this paper is to extend our previous report on variation in dental occlusion within groups of Bougainville Island, Papua New Guinea (Smith and Bailit, '77b) to a consideration of microdifferentiation among groups. Particular emphasis is placed on the geographic pattern and magnitude of this diversity, on its relationship to variation in other biological systems, and on an evaluation of its biological significance.

MATERIALS AND METHODS

Sample selection

Bougainville is the northernmost of the Solomon Islands in the South Pacific. This study concerns 14 villages distributed along a 60 mile range in the central region of the island (Fig. 1). Included are twelve Papuan (non-Austronesian) speaking villages used as a pooled sample for a descriptive analysis of within-group variation (Smith and Bailit, '77b), plus two shore-line Austronesian populations (Table 1). Additional information regarding linguistics, geography and ecology of these villages can be found in Friedlaender ('75).

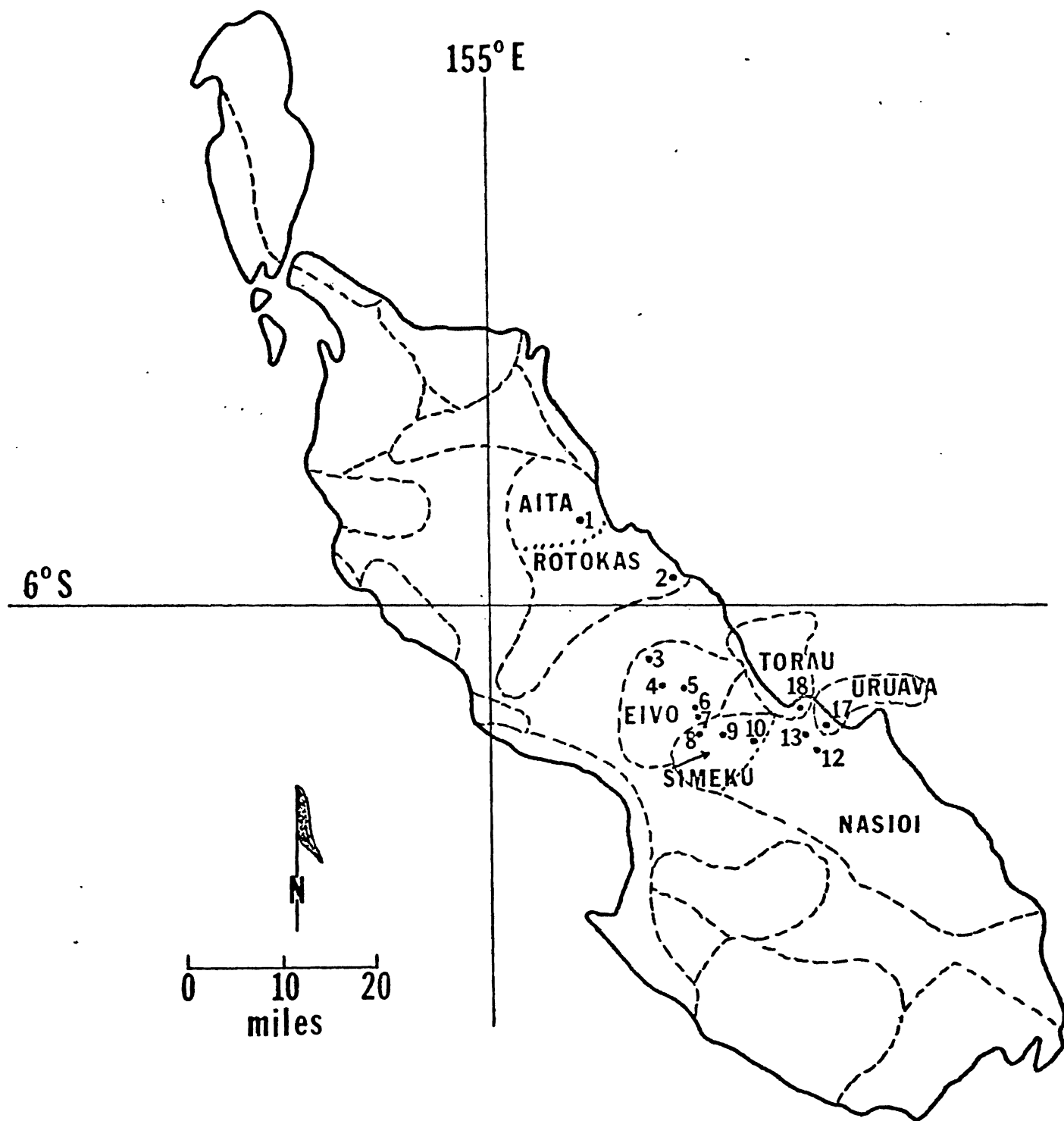
Data collection

The collection of dental casts and measurement definitions, techniques, and reliability have been described previously (Smith and Bailit, '77b). The twenty occlusal and arch size variables include:

Occlusal variables

Overjet

Overbite or openbite



Sagittal molar relationship

Upper anterior crowding or spacing

Lower anterior crowding or spacing

Upper rotations and displacements

Lower rotations and displacements

Midline diastema

Posterior openbite

Posterior crossbite

Arch size

Upper intercanine width

Upper intermolar width

Lower intercanine width

Lower intermolar width

Upper arch length

Lower arch length

Computed ratios

Upper shape (upper intermolar width/upper arch length) x 100

Lower shape (lower intermolar width/lower arch length) x 100

Upper width ratio (upper intercanine width/upper intermolar width) x 100

Lower width ratio (lower intercanine width/lower intermolar width) x 100

Ascertainment

Approximately 1200 sets of dental casts were collected during the summer of 1970. Because of variation in eruption timing and sequence during the mixed dentition period, the sample was restricted to 941 subjects with permanent (adult) dentitions. Interpolation from 1963 census figures and populations pyramids (Friedlaender, '75) indicated an ascertainment of approximately 51%

(941 of 1838) for subjects over age 12 (Table 1). This estimate is conservative, taking no account of deaths between 1963 and 1970 or of edentulous subjects from whom casts were not taken. The problem of incomplete sampling is both universal and unavoidable for large populations studied under field conditions.

Individuals used in the data analysis were further restricted to those with complete permanent dentitions, with or without third molars. We have discussed elsewhere (Smith and Bailit, '77a) the problems resulting from tooth loss in population studies of dental occlusion. In brief, it probably results in some reduction in total variation, with a tendency toward elimination of extreme scores. The final village sample sizes and the number of subjects excluded because of missing teeth are listed in Table 1.

Data preparation

A correction was made for age-related variation among individuals, which accounted for almost 25% of the total variation in some arch shape ratios, but generally less than 15% for most individual measurements (Smith and Bailit, '77b). Using polynomial regression equations, calculated separately by sex for each variable, measurements were standardized to values predicted at 30 years of age. All data presented in this report refer to age-adjusted rather than raw scores. For approximately 20% of subjects, age determinations were not made in the field and have been estimated from genealogical data and the appearance of the dentition.

Each variable was examined separately by sex for non-normality and homogeneity of variance among villages. Constants were first added to make all values positive, eliminating logarithmic transformations of negative values. The mild skewness and kurtosis (as determined by third and fourth sample moments) for upper and lower rotation and displacement scores, upper and lower arch shape ratios, and the upper arch width ratio were improved by logarithmic transformations in both sexes. Midline diastema, posterior openbite and posterior cross-bite

Table 1

Distribution and Ascertainment of Subjects

Village ¹	Estimated 1970 Adult Census	% Sampled	Number of adults with complete dentitions		Number of adults with missing teeth		% with missing teeth
	M+F	M+F	M	F	M	F	M+F
Nupatoro	138	25.4	18	11	4	2	17.1
Okowopaia	108	52.8	21	19	7	10	29.8
Kopani	204	54.9	40	56	12	4	14.3
Kopikiri	79	60.8	16	23	5	4	18.8
Nasiwoiwa	112	77.7	36	40	7	4	12.6
Atamo	201	59.7	29	31	8	4	17.5
Uruto			18	21	7	2	
Karnavitu	136	72.1	42	41	10	5	15.3
Boira	98	57.1	28	26	2	1	5.3
Korpei	196	50.5	36	54	9	10	17.4
Pomaua	148	37.8	23	24	7	2	16.1
Bairima	61	54.1	12	13	3	5	24.2
Arawa	113	28.3	9	18	4	1	15.6
Rorovana	244	39.8	23	35	16	23	40.2
Totals	1838	51.2	351	412	101	77	18.9

¹ Village numbers correspond to Friedlaender ('75) and Figure 1.

were not sufficiently improved by any transformation to allow inclusion of these variables in the multivariate analysis. All other variables were left in their original scale of measurement.

Data analysis

Calculations were performed using SPSS (Nie et al., '75) and BMDP (Dixon, '75) programs. For verification, analyses were obtained from both packages and compared whenever possible.

Clinal variation. An evaluation of clinal variation was made on the ten villages of the Eivo, Simeku and Nasioi languages (Table 1, Figure 1), which are arranged in a generally linear pattern. Because of the inhospitable geographic region isolating the Aita and Rotokas villages and the linguistic and cultural distinctions of the Torau and Urawa, these villages have highly restricted gene flow with all others, and were therefore excluded from the analysis of clinal variation.

Villages were assigned ordinal numbers according to position (Rhoads and Friedlaender, '75), number one being the northernmost Eivo village, Kopani, and 10 the southern Nasioi village, Pomaua. These numbers were then correlated with individual scores for each variable, using a non-parametric measure, Spearman's rho. Positive clines indicate an increase in values from north to south and negative clines a decrease.

Hierarchical analysis of variance. Rhoads and Friedlaender ('75) have demonstrated that Bougainville is organized as a two-fold hierarchical subdivision of the breeding population, in which each measurement can be considered to result from the linear combination of three additive effects, due to the (a) language group, (b) village, and (c) unique characteristics of the individual.

The components of variation in this model have been evaluated by a two-level nested Model II (random effects) analysis of variance (Sokal and Rohlf, '69),

in which individuals are nested within villages and villages within languages. Program P2V of the BMDP series was used for these calculations. However, this program computes F ratios by placing the mean square of each nested factor over the error term. Since the expected mean square at each level contains the variation from all lower levels (Sokal and Rohlf, '69), the F ratios for the significance of differences among languages were recalculated using the village rather than error mean square in the denominator. The nonorthogonality of expected mean squares and variance components resulting from unequal sample sizes was treated following the methods of Sokal and Rohlf ('69).

Discriminant analysis. The multivariate pattern of divergence among villages was examined by linear discriminant functions (canonical variates) analysis. These calculations were performed separately on three subgroups of the total set of dependent variables: (1) the seven occlusal variables, (2) the six arch size measurements, and (3) the combined data set of 13 variables. The significance of overall discrimination was evaluated with Rao's F approximation for Wilk's Lambda, which tests the hypothesis of equality among population centroids.

Synthesis. Friedlaender ('75) has evaluated the similarity among distance matrices based on anthropometrics, tooth size, dermatoglyphics, blood genetics, geographic distance, linguistics and migration rates for the natives of these villages. The purpose of this section is to determine how the pattern of divergence among villages for the characteristics of dental occlusion compares to these previously established relationships.

A matrix of distances, calculated separately by sex for each of the three subgroups of variables examined by discriminant analysis, was correlated with the other matrices using Spearman's rho. When calculated from triangular distance matrices based on multivariate observations, this statistic is normally distributed for the null case, and is tested with N-1 degrees of freedom, N

being the number of paired comparisons, in this case, 91 (Lingoes, '73). Mahalanobis D^2 distances were used for anthropometrics, tooth size, dermatoglyphics and the variables analyzed in the present study. Blood genetic, geographic, linguistic and migrational distances are as described by Friedlaender ('75).

It is important that variables in each data set are uncorrelated with variables in other sets when measured on individuals within villages (Neel et al., '74). If significant relationships exist, correlations among distance matrices may reflect no more than correlations among variables. In fact, the presence of several highly significant within-group correlations between the variables in this study and those in the anthropometric and tooth size data sets suggests that comparisons among these matrices would be inappropriate.

RESULTS

Univariate Differences

The analysis of variance for differences among the 14 villages for each variable is presented in Table 2. In general the highest F ratios are for arch lengths and widths. Significant differences among villages are found for all of these measurements. Except for lower intermolar width, the F ratios are all higher in females than in males. The four ratio variables, describing arch "shape", are no more variable among villages than the linear measurements on which they are based.

The occlusal variables are not consistent in their pattern of differentiation. Except for the sagittal molar relationship and posterior cross-bite, all occlusal variables reach statistical significance in one sex but not in the other.

Table 2

Univariate Patterns of Geographic Microdifferentiation

	Analysis of Variance		Clines		Percentage of total variation accounted for by each level			
	F ratios among 14 villages		Spearman's rho for individual scores		Hierarchical Analysis of Variance			
	Males N=351	Females N=412	Males N=280	Females N=329	Among Languages Villages	Among Individuals	Among Languages Villages	Among Individuals
Overjet	3.26**	0.61	0.03	0.03	-	91.0	-	100.0
Overbite	3.08**	1.57	-0.13*	-0.10*	-	89.6	0.7	97.6
Molar relationship	1.26	0.76	0.05	-0.02	2.1	97.9	-	100.0
Upper crowding or spacing	1.56	2.01*	-0.12*	-0.09*	-	97.3	-	95.9
Lower crowding or spacing	0.61	2.44**	-0.01	0.09	-	100.0	0.2	94.6
Upper rotations and displacements (log)	1.58	3.58**	0.07	-0.02	-	97.2	-	89.3
Lower rotations and displacements (log)	1.33	1.75*	0.02	-0.10*	-	98.2	-	97.0
Midline diastema (reciprocal)	1.73*	1.33	0.05	0.08	-	95.5	-	97.7
Posterior openbite (reciprocal)	3.76**	1.45	0.18**	-0.02	-	89.2	-	97.7
Posterior cross-bite	1.61	1.30	-0.16**	-0.05	3.3	86.7	-	98.6
Upper canine arch width	4.57**	5.99**	-0.24**	-0.28**	10.3	83.3	6.1	85.9
Upper molar arch width	2.69**	2.83**	-0.13*	-0.20**	2.4	93.5	1.8	94.6
Lower canine arch width	3.26**	4.51**	-0.09	-0.11*	-	90.1	-	92.7
Lower molar arch width	3.38**	2.73**	-0.21**	-0.24**	2.5	89.9	2.0	94.6
Upper arch length	3.31**	5.83**	-0.05	-0.16**	4.8	90.1	2.9	86.9
Lower arch length	2.90**	5.31**	-0.04	-0.14**	0.4	92.6	1.4	88.5
Upper arch shape ratio (log)	1.42	3.36**	0.07	0.04	2.6	97.4	1.8	95.4
Lower arch shape ratio (log)	2.82**	4.22**	0.15**	0.09*	-	94.1	0.8	93.3
Upper arch width ratio (log)	3.52**	3.35**	-0.18**	-0.16**	6.7	91.3	1.2	94.4
Lower arch width ratio	1.95*	3.19**	0.05	0.07	-	95.5	-	97.7

p < 0.05 ** p < 0.01

Clinal Variation

All arch width and length measures decrease from north to south (Table 2). In both sexes, this trend is strongest for upper canine arch width, followed by lower molar arch width. Because of the elimination of individual variation, clines based on village means were much higher than those reported in Table 2 for individual scores, but did not generally reach statistical significance because they were associated with only 8 degrees of freedom. Inspection of these village means, however, suggests that clines are not smooth across the region but occur primarily at language boundaries. The pattern of size change from north to south for arch width measurements is very similar to that described by Friedlaender ('75) for bizygomatic width.

Hierarchical Analysis of Variance

Most of the variation for the characteristics of dental occlusion on Bougainville exists among individuals rather than between groups (Table 2). Variation that can be accounted for by language differences generally ranges from 0 to 4% of total variation, while village-within-language differences are most frequently in the 2 to 10% range. Although averages of language and village effects are not entirely valid because variables are not independent, the mean percentage of total variation for the 20 measurements due to language differences is 1.8% in males and 1.0% in females, while villages account for 5.1% and 4.6%. For occlusal variables, little variation is due to language effects in either sex.

Multivariate Analysis.

The summary results for these analyses and a comparison with Friedlaender's ('75) data are given in Table 3. The data sets are listed in order of significance of the overall discrimination among populations. The combined set of occlusal

Table 3

Summary table for linear discriminant analyses of 14 villages

Data Set	Number of Variables	Number of Subjects	Wilks Lambda	Rao's F	df ₁	df ₂	Probability	% Classified Correctly
(Anthropometry)	13	526	0.1585	5.03	169	3866	5.38×10^{-80}	37.6 (18 villages)
(Male Dentometrics)	21	418	0.2401	2.16	273	4298	4.68×10^{-23}	35.7
(Female Dentometrics)	21	428	0.3005	2.04	273	4864	6.32×10^{-20}	-
Male Combined Occlusal and Arch Size	13	351	0.3253	2.31	169	3033	6.22×10^{-18}	29.3
Female Combined Occlusal and Arch Size	13	412	0.3710	2.50	169	3619	3.05×10^{-21}	27.2
(Male Dermatoglyphics)	28	675	0.4145	1.37	364	6463	6.65×10^{-6}	24.5 (18 villages)
(Female Dermatoglyphics)	28	697	0.4243	1.42	364	6864	5.18×10^{-7}	24.6 (17 villages)
Male Arch Size	6	351	0.5411	2.77	78	1837	7.85×10^{-14}	21.4
Female Arch Size	6	412	0.5687	3.01	78	2179	1.90×10^{-16}	19.2
Male Occlusion	7	351	0.6227	1.80	91	2072	8.58×10^{-6}	19.1
Female Occlusion	7	412	0.6592	1.87	91	2456	1.86×10^{-6}	17.2

Data sets in () from Friedlaender, '75. All probabilities recalculated with Hewlett-Packard Continuous Distribution Pack. Data are for analysis of same 14 villages except for percentage classified correctly, where indicated.

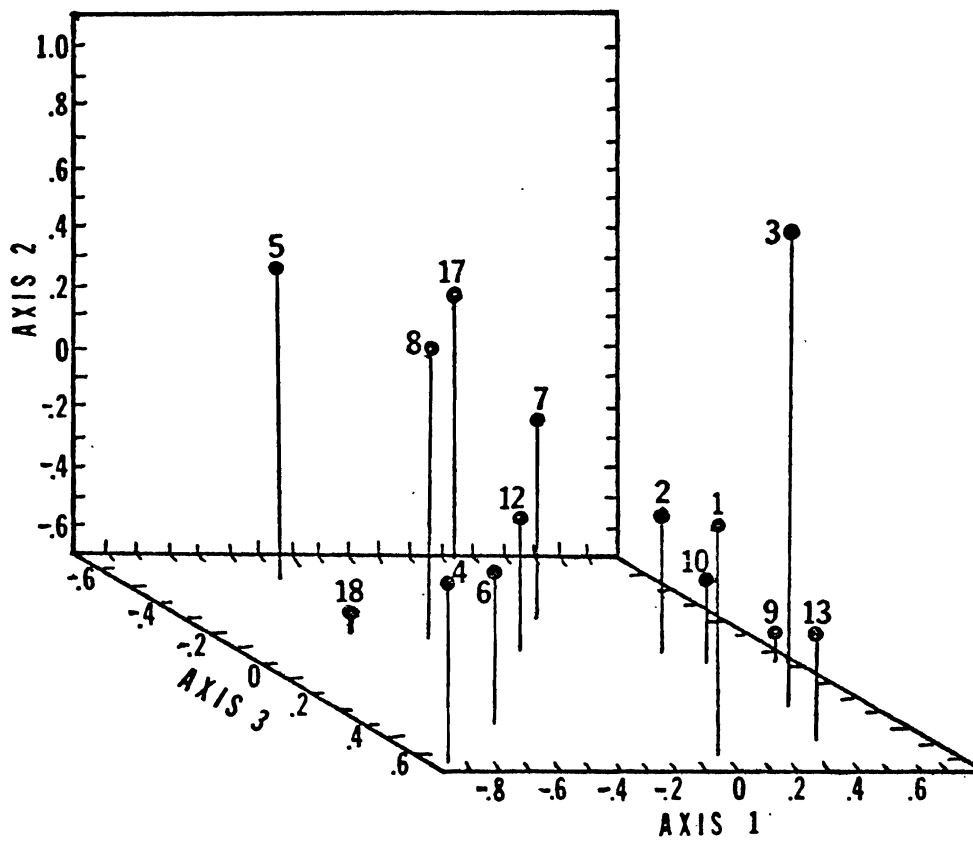
Table 4

Standardized Discriminant Coefficients and Discriminant Loadings
for Combined Data Set (Males).

	Standardized Coefficients				Discriminant Loadings			
	Function 1	Function 2	Function 3	Function 4	Function 1	Function 2	Function 3	Function 4
Overjet	-0.365	-0.921	-1.266	-0.043	-0.436	-0.099	-0.532	0.055
Overbite	-0.509	-0.102	0.555	-0.357	-0.552	0.106	-0.114	-0.307
Sagittal molar relationship	-0.388	-0.867	-0.232	-0.143	-0.003	-0.041	0.253	-0.031
Upper crowding or spacing	-0.119	0.012	0.522	-0.477	-0.264	0.140	0.229	-0.368
Lower crowding or spacing	0.050	-0.100	-0.756	0.292	-0.078	-0.146	-0.087	-0.086
Upper rotations and displacements	0.001	-0.069	0.609	0.132	0.031	-0.170	0.250	0.251
Lower rotations and displacements	-0.154	-0.081	0.312	0.042	-0.075	-0.070	0.366	0.263
Upper canine arch width	-0.154	1.205	-0.369	0.780	-0.694	0.188	-0.019	0.366
Upper molar arch width	0.188	-1.540	-0.131	-0.033	-0.542	-0.139	0.070	0.397
Lower canine arch width	-0.384	-0.730	0.042	-0.946	-0.636	-0.151	0.033	-0.022
Lower molar arch width	-0.482	1.322	0.078	0.182	-0.615	0.052	0.071	0.285
Upper arch length	0.316	1.758	0.867	0.325	-0.519	-0.196	0.107	0.551
Lower arch length	-0.337	-1.930	-0.220	0.280	-0.406	-0.297	0.196	0.606

and arch size variables are clearly superior to dermatoglyphic traits for discriminating among these populations and for classifying individuals, particularly considering that only 13 occlusal and arch size variables were used in comparison to 28 dermatoglyphic traits. The present variables, however, are distinctly inferior to anthropometrics and roughly similar to tooth size, if differences in the number of variables are again considered. The six arch size measurements provide better discrimination than the seven occlusal variables, even though the intercorrelations among the arch size subset are higher.

The standardized discriminant function coefficients, and the discriminant loadings for the four significant functions used to classify males from the total data set are presented in Table 4. The standardized discriminant coefficients are used to calculate discriminant scores from standardized variates, and have usually been the basis for the interpretation of discriminant functions. As discussed by others (Howells, '73; Friedlaender, '75; Rightmire, '75), better interpretation is usually provided by discriminant loadings, which are the the correlations of each variable with the discriminant scores. The first discriminant function separates villages on the general size of the dental arches, but also includes large effects of overjet and overbite. The second function is unusual and difficult to interpret. No loading is greater than .30, and only lower arch length exceed .20. The third function separates individuals with little overjet, molar relationships in the direction of mandibular prognathism and rotated and displaced teeth from subjects with large overjet and distally positioned mandibular molars. The last significant function primarily concerns the length of the upper and lower arches but with a number of additional measurements added to these features. The distribution of villages in space on the first three functions, which account for 66% of total discrimination, is presented in Figure 2.



Synthesis

The pattern of microdifferentiation for dental occlusion and the size of the dental arches is largely unrelated to the pattern of differentiation for other biological systems or to measures which reflect gene flow (Table 5). Distance matrices for males and females are highly correlated on both occlusion and arch size (male occlusion with female occlusion, $r = .45$; male arch size with female arch size, $r = .60$), but the relationship between occlusion and arch size distances are low both within and among sexes (Table 6).

DISCUSSION

This study has addressed several problems related to dental occlusion. First, how much do these traits vary and why? Second, how useful are these measurements for discriminating among human groups? Third, to quote Spielman and Smouse ('76), "Are the differences between human populations biologically meaningful, or are they unimportant compared to variation within a single population"?

It is important to note that many aspects of this discussion are valid only for this population. However, we expect that some generalization is possible. Results from similar studies are likely to differ in degree more than in kind. On the other hand, the results cannot at all be generalized to variation at other levels. The differences among populations over large environmental ranges may be related to entirely different mechanisms from those discussed here.

What can be said about the biology of occlusal characteristics and arch size? First, they do seem to be distinct sets of variables; the principal difference being the random variability associated with the occlusal characteristics. Occlusal variables show little correspondence between sexes in the degree of univariate differences among villages or in the magnitude of

Table 5

Congruence between occlusal and arch size distance matrices

and distances from Friedlaender, '75. Spearman's rho

	Males			Females		
	Combined Occlusion and Arch Size	Occlusion only	Arch Size only	Combined Occlusion and Arch Size	Occlusion only	Arch Size only
Anthropometry	0.09	0.10	0.05	0.11	0.12	0.04
Male Teeth	-0.05	-0.02	0.10	-0.05	-0.13	0.10
Female Teeth	0.26	0.30	0.02	0.18	0.20	0.23
Male Dermatoglyphics	-0.18	-0.05	-0.15	-0.20	-0.16	-0.18
Female Dermatoglyphics	-0.11	-0.07	-0.06	0.10	-0.28	0.30
Blood	-0.10	0.06	-0.10	-0.02	-0.11	0.16
Geography	-0.08	0.08	-0.11	-0.09	-0.07	0.03
Language	0.16	0.12	0.15	0.08	0.18	-0.01
Migration	0.16	0.15	0.16	0.13	0.03	0.17

Table 6

Congruence between distance matrices for occlusal
and arch size variables, Spearman's rho

	Male Occlusion	Female Occlusion	Male Arch Size
Female Occlusion	0.45		
Male Arch Size	0.31	0.14	
Female Arch Size	0.13	0.16	0.60

clines. Unlike arch size and other anthropometrics (Rhoads and Friedlaender, '75), there is little indication of any language effect when the variance is partitioned, and they are poor indicators of variation among populations.

In sum, the results confirm previous observations (Smith and Bailit, '77b), which suggested that measurements of arch size behaved as relatively typical craniometric traits, while for occlusal characteristics, the large variation within populations seems to obscure differences between populations, and the variation within populations probably has a large component related to the random effects associated with individual developmental histories. In Waddington's terms ('57), dental occlusion is a relatively poorly canalized system. This is further suggested by a high magnitude of bilateral asymmetry for these traits (Smith and Bailit, in preparation).

The usefulness of occlusal variables and arch measurements for discriminating among groups at this microevolutionary level is quite limited. In studies of tooth morphology, Sofaer et al. ('72) and Brewer-Carias et al. ('76), agreed that the "value of tooth morphology as an indicator of genetic differences between populations can be viewed with cautious optimism." We are not as optimistic regarding their results or our own. Even the strongest relationship observed between village distances, .60 for dental morphology with genetic markers by Brewer-Carias et al. ('76), still leaves much of the variance in these distances unexplained, and the correct classification of 30% of subjects by occlusal and arch size variables in the present study is an entirely unsatisfactory percentage for any practical attempts at identification. The poor performance of arch size measurements and their low correlations with genetic and geographic distances were surprising. It may be that this small number of variables, all highly intercorrelated, contained inadequate information to be representative. Based on our data and previous studies, it appears

that there is little reason to be optimistic about the ability of the dentition to identify group membership at the level of microdifferentiation considered here. Of course, for more diverse groups, dental morphology and tooth size are of widely recognized and demonstrated value (eg., Riesenfeld, '56; Baillit et al., '68; Palomino et al., '77), while little is known about dental occlusion in this regard.

Are the differences among populations biologically meaningful? This perhaps depends upon the definition of meaningful. While we recognize that variation among populations due to stochastic processes is important, biological meaningfulness largely implies to us variation of functional (i.e., adaptive) significance.

From this viewpoint, it is becoming clear, both at the microevolutionary (Rhoads and Friedlaender, '75; the present study) and species level (Lewontin, '73) that for most characteristics taken one at a time, the overwhelming majority of human variation occurs among individuals within groups, and is unlikely to be biologically significant. Spielman and Smouse ('76) have contrasted this univariate approach with patterns of multivariate divergence among populations. Since single measurements may not describe functionally significant characteristics, we agree that a multivariate analysis is theoretically preferable.

However, there are problems with the application of a multivariate approach. One method frequently used to judge the success of multivariate population discrimination has been the number of subjects correctly classified (Friedlaender, '75; Rightmire, '75; Spielman and Smouse, '76). It is generally assumed that on a random basis this percentage depends simply on the number of villages, eg., 1/14 or 7.14% in the present study; but this null hypothesis does not take into account chance variation used by the discriminant function in allocation. As a preliminary demonstration of this problem, each male subject was assigned variables generated from a table of random numbers. Four trials were

run with each of 6, 7 and 13 variables. The percentage correctly classified by this procedure exceeded the expected 7.1%:

Number of random variables used to generate discriminant functions	% classified into correct 1 of 14 villages	
	\bar{X}	Range (4 trials)
6	12.9	11.4 - 14.0
7	14.0	11.4 - 15.4
13	18.8	16.8 - 22.2

A discriminant analysis is clearly capable of taking advantage of nonsense variation present in random numbers to assign subjects to correct groups. The effect of number of subjects, variables and groups on the percentage of correctly classified subjects needs to be worked out in detail in order to establish valid null hypotheses for this type of analysis.

Even without appropriate null estimates, there are many examples in the literature where correct allocations exceed the possible range of random expectations. Spielman and Smouse ('76) found that 18 characteristics could correctly classify 41% of Yanomama Indians among 19 villages. They suggest that this represents meaningful biological diversification, but we disagree. It is important here to distinguish between taxonomic and biologic "meaningfulness". Their 18 variables include 6 genetic markers and 12 anthropometric traits, such as sitting height, calf circumference and nose height and breadth. This artificial combination of variables results in discriminant functions that are taxonomically useful, but no functional interpretation can be applied to a linear combination of these unrelated traits. If an attempt is going to be made to apply multivariate analysis to biological differences among populations, more attention must be directed toward restricting data sets to variables which interact in a functionally interpretable manner. In addition, rather than explaining

divergence on an a posteriori basis, after it has been observed, it would be far more convincing to formulate a priori biological hypotheses indicating why adaptive variation among populations might exist, and to then confirm its presence.

However, populations such as the Xavante, Yanomama and those on Bougainville have been of interest largely because they are assumed to be unlikely places for selective differences to occur. Gould and Johnston ('72) have observed that "there is a confusing nongenetic cause of phenetic variation that will usually operate in precisely the same sense as selectively ordered genetic variation: direct modification by the environment." This problem leads those interested in genetic differences to these areas precisely because it can be postulated that confounding environmental effects are not present (eg., Friedlaender et al., '71). However, without environmental variation, there can be no selectively determined differences either. By default, variation among groups in these studies can only be attributed to founder effects, gene flow or genetic drift. While such studies have been of value by verifying that theoretical processes such as drift may be important in human populations, they are not appropriate for drawing conclusions about the causes for variation among groups, since the presence or absence of alternative causes are assumed by the analysis.

FIGURE LEGENDS

Figure 1. The island of Bougainville in the Solomon Islands, Papua New Guinea. The language groups and villages included in this study are indicated (from Friedlaender, '75).

Figure 2. Village centroids (means) on first three discriminant functions for analysis of combined data set of males. These axes account for 29%, 25% and 12% of the total variation among villages.

LITERATURE CITED

- Bailit, H.L., S.J., DeWitt and R.A. Leigh 1968 The size and morphology of the Nasioi dentition. *Am. J. Phys. Anthropol.* 28: 271-288.
- Boyd, R.C. 1972 An odontometric and observational assessment of the dentition. In: R.A. Littlewood, *Physical Anthropology of the Eastern Highlands of New Guinea*. Univ. Washington Press, Seattle. pp. 175-212.
- Brewer-Carias, C.A., S. LeBlanc and J.V. Neel 1976 Genetic structure of a tribal population, the Yanomama Indians. XIII. Dental microdifferentiation. *Am. J. Phys. Anthropol.* 44: 5-14.
- Dixon, W.J., ed. 1975 BMDP Biomedical Computer Programs. Univ. Calif. Press, Berkeley.
- Friedlaender, J.S. 1975 *Patterns of Human Variation*. Harvard Univ. Press, Cambridge.
- Friedlaender, J.S., L.A. Sgaramella-Zonta, K.K. Kidd, L.Y.C. Lai, P. Clark and R.J. Walsh 1971 Biological divergences in south-central Bougainville: an analysis of blood polymorphism gene frequencies and anthropometric measurements utilizing tree models, and a comparison of these variables with linguistic, geographic, and migrational "distances." *Am. J. Hum. Genet.* 23: 253-270.
- Gould, S.J. and R.F. Johnston 1972 Geographic variation. *Ann. Rev. Ecol. Systemat.* 3: 457-498.
- Guttman, R., L. Guttman and K.A. Rosenzweig 1967 Cross-ethnic variation in dental, sensory and perceptual traits: a nonmetric multibivariate derivation of distances for ethnic groups and traits. *Am. J. Phys. Anthropol.* 27: 259-276.
- Howells, W.W. 1973 *Cranial Variation in Man*. Papers Peabody Museum Arch. Ethnol., Harvard Univ., Vol. 67.

- Lewontin, R.C. 1973 The apportionment of human diversity. *Evol. Biol.* 6: 381-398.
- Lingoes, J.C. 1973 cited by Neel, J.V., F. Rothhammer and J.C. Lingoes. *Am. J. Hum. Genet.* 26: 281-303, 1974.
- Neel, J.V., F. Rothhammer and J.C. Lingoes 1974 The genetic structure of a tribal population, the Yanomama Indians. X. Agreement between representatives of village distances based on different sets of characteristics. *Am. J. Hum. Genet.* 26: 281-303.
- Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner and D.H. Bent 1975 *SPSS Statistical Package for the Social Sciences*, 2nd Ed. McGraw-Hill Book Co., New York.
- Palomino, H., R. Chakraborty and F. Rothhammer 1977 Dental morphology and population diversity. *Human Biol.* 49: 61-70.
- Rhoads, J.G. and J.S. Friedlaender 1975 Language boundaries and biological differentiation on Bougainville: multivariate analysis of variance. *Proc. Nat. Acad. Sci., USA* 72: 2247-2250.
- Riesenfeld, A. 1956 Shovel-shaped incisors and a few other dental features among the natives of the Pacific. *Am. J. Phys. Anthropol.* 14: 505-521.
- Rightmire, G.P. 1975 New studies of post-pleistocene human skeletal remains from the Rift Valley, Kenya. *Am. J. Phys. Anthropol.* 42: 351-370.
- Simpson, G.G. 1953 *The Major Features of Evolution*. Columbia Univ. Press, New York.
- Smith, R.J. and H.L. Bailit 1977a Problems and methods in research on the genetics of dental occlusion. *Angle Orthodont.* 47: 65-77.
- Smith, R.J. and H.L. Bailit 1977b Variation in dental occlusion and arches among Melanesians of Bougainville Island, Papua New Guinea. I. Methods, age changes, sex differences and population comparisons. *Am. J. Phys. Anthropol.* In Press,

- Sofaer, J.A., J.D. Niswander, C.J. MacLean and P.L. Workman 1972 Population studies on southwestern Indian tribes. V. Tooth morphology as an indicator of biological distance. *Am. J. Phys. Anthropol.* 37: 357-366.
- Sokal, R.R. and F.J. Rohlf 1969 *Biometry*. W.H. Freeman and Co., San Francisco.
- Spielman, R.S. and P.E. Smouse 1976 Multivariate classification of human populations. I. Allocation of Yanomama Indians to villages. *Am. J. Hum. Genet.* 28: 317-331.
- Waddington, C.H. 1957 *The Strategy of the Genes*. Allen and Unwin, London.